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THE HORNED LIZARDS OF CALIFORNIA
AND NEVADA OF THE GENERA
PHRYNOSOMA AND *ANOTA*

BY

HAROLD C. BRYANT

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* The present paper is the result of work carried on in the Department of Zoology of the University of California as partial fulfillment of the requirements for the master's degree, under the direction of Professor Charles A. Kofoid.

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INTRODUCTION

The paper here presented is the result of preliminary study of *Phrynosoma blainvilliei* carried on at Pomona College during 1908 and a further study of the five species of *Phrynosoma* known to inhabit the states of California and Nevada, conducted at the University of California during the college year 1909-1910.

The material upon which this study is based consists of a good working collection of some sixty alcoholic specimens, representing ten of the known species of *Phrynosoma*, belonging to the Zoological Department of the University of California, and in addition a collection of over one hundred and fifty specimens, representing four of the species under consideration, belonging to the Museum of Vertebrate Zoology of the University of California. A cursory examination, which threw new light on the subject, was made of the collection in Leland Stanford Junior University. In all some three hundred specimens were examined. Observation of a large number of live specimens in the field and in the laboratory furnished the foundation for most of the habit notes.

To Professor C. A. Kofoid, under whose direction the work was done, Professor J. C. Merriam, Professor H. B. Torrey, and

Dr. J. A. Long of the University of California, Mr. Joseph Grinnell of the Museum of Vertebrate Zoology, and to Professor J. O. Snyder of Leland Stanford Junior University, the author is greatly indebted for use of material and for valuable suggestions. Thanks are also due Miss Elizabeth Heald for the text figures.

GENERAL DISCUSSION OF THE GENUS

GENERIC CHARACTERS

The southwestern part of the United States, with its warm, dry climate and great deserts, affords most favorable conditions for many of our reptiles. Among the Lacertilia to be found in this locality, no group is so unique and specialized as the genus *Phrynosoma*. The members of this genus are easily distinguished from the other lizards by their flat, oval bodies, covered with keeled, spiny scales, and by their circlet of horns upon the head. Their round pupils, numerous series of ventral scales not abruptly smaller than the laterals, notched tongue and femoral pores, place this genus among the Iguanidae. The presence of horns, however, widely separates the genus from the remainder of this family.

The members of the genus *Phrynosoma* are commonly known as "horned toads." The first part of this name describes these lizards very well, but the last is a misnomer for they bear no close relation to the batrachians. No doubt their sluggish habits and method of obtaining food by means of a viscid tongue, offer an explanation for this misnomer. From a scientific standpoint the name "horned lizard" is far more appropriate.

HISTORICAL DISCUSSION

Clavigero (1780), in his "Storio del Messico," describes and figures a Mexican horned lizard. He describes it thus, "It is remarkable for its shape, being perfectly round and cartilaginous; the body is six inches in diameter; the head is hard and spotted with various colors." His crude figure shows eight spines on the occiput and six transverse bands on the back. Hernandez (1790) also describes and figures a horned lizard from Mexico. Both of these men gave it the Mexican name, *Tepajaxin*. Later, several others (Barton, 1807!; Wood, 1871) used this term specifically.

Harlan (1825) was the first one to class the horned lizards in the genus *Agama*, his reason for so doing being the presence of femoral pores. He described the Texas horned lizard under the name *Agama cornuta*, calling attention to the fact that "It approaches nearest the *Agama orbicularis* Daudin (1802) or the *Lacerta orbicularis* Linnaeus (1787), the Tapayaxin of Seba, who has given three figures of the species." Four years later, Harlan (1829), in a synopsis of the reptiles of North America, describes but one species, *Agama cornuta* and gives its distribution as "transmississippi territories as far west as the plains of the Columbia River, and as far south as Arkansa [sic!]."

The Oregon horned lizard, *Phrynosoma douglassi*, was also placed in the genus *Agama* by Bell (1828). In the same year Wiegmann (1828) placed all of the known horned lizards in a new genus by themselves which he termed *Phrynosoma*. Girard (1858) divided this genus into four subgenera, *Tapaya*, *Batrachosoma*, *Phrynosoma*, and *Doliosaurus*. The subgeneric characters not being diagnostic, but few have used this classification. Cope (1898), instead of following the classification of Girard, divided the genus into two genera, *Phrynosoma* and *Anota*, basing the division on the character of the auricular aperture. This would seem to be the best division that could be made were it not for the numerous instances of intergradation to be found. Both *Phrynosoma platyrhinos* and *P. modestum*, two species grouped under the genus *Anota* in which the tympanum is concealed by a scaly integument, show wide variation in this respect, all gradations from an almost naked tympanum to one entirely concealed being found within each species.

One grouping used by Cope (1898) and Van Denburgh (1897) based on the position of the nostrils, divides the species into well defined groups, but those within each group are so unlike in other characteristics and in distribution that even this division is unsatisfactory.

The bases for generic and specific distinction among the horned lizards have not as yet been generally accepted owing to this difficulty experienced in finding dependable characters.

The working out of a key from a complete set of specimens of all the species might reveal the necessary characters for a revision of the genus. Until this can be done, the classification used by most of the recent writers (Gentry, 1885; Van Denburgh, 1897; Ditmars, 1907), grouping all of the species under the one genus *Phrynosoma*, is best used. One exception, that of *Anota maccalli* (*Phrynosoma maccalli*), should be made. It is here placed by itself in the genus *Anota*, the reasons being given in their proper place.

In the following table are given the recognized species and subspecies of the two genera with their distribution.

**A LIST OF THE RECOGNIZED SPECIES AND SUBSPECIES OF THE
GENERA PHRYNOSOMA AND ANOTA**

Species	Distribution
1. <i>Phrynosoma asio</i> Cope	Southwestern Mexico
2. <i>Phrynosoma blainvillici</i> blainvillici (Gray) Bryant	Southern California
3. <i>Phrynosoma blainvillici</i> frontale (Van Denburgh) Bryant	Central California
4. <i>Phrynosoma boucardi</i> Bocourt	Plateau of Mexico
5. <i>Phrynosoma braconnieri</i> Bocourt	Southern Mexico
6. <i>Phrynosoma cerroense</i> Stejneger	Cerro Island, Lower California
7. <i>Phrynosoma cornutum</i> Harlan	Kansas, Oklahoma, Texas, New Mexico and Northern Mexico
8. <i>Phrynosoma coronatum</i> Blainville	Lower California
9. <i>Phrynosoma ditmarsi</i> Stejneger	Sonora, Mexico
10. <i>Phrynosoma douglassi</i> douglassi (Bell) Stejneger	Northern part of Pacific Region
11. <i>Phrynosoma douglassi</i> hernandesi (Girard) Cope	Great Plains and Rocky Mountains
12. <i>Phrynosoma douglassi</i> ornatissimum (Girard) Cope	Painted Desert of Arizona
13. <i>Phrynosoma goodei</i> Stejneger	Sonora, Mexico
14. <i>Phrynosoma modestum</i> Girard	Texas, New Mexico, Utah, Arizona and southwestern Mexico
15. <i>Phrynosoma orbiculare</i> Wiegmann	Plateaus of Mexico
16. <i>Phrynosoma platyrhinos</i> Girard	Lower Sonora and Deserts of the Great Basin from California to Utah
17. <i>Phrynosoma solare</i> Gray	Valleys of the Gila and Colorado rivers
18. <i>Phrynosoma taurus</i> Duges	Southeastern Mexico
19. <i>Anota maccalli</i> Hallowell	Deserts of the Gila and Colorado rivers

Genus **Phrynosoma** Wiegmann

Anotia, Cope (1866), p. 310.

Tapaya Girard (1858), pp. 394-399, pl. 21, figs. 6-9.

Batrachosoma Girard (1858), pp. 354-365, pl. 20, figs. 10-13.

Dolosaurus Girard (1858), pp. 407-410.

Many good descriptions of the genus *Phrynosoma* are to be found, but all except Cope's (1898) are based solely on external characters. It is hoped that the addition here made of the more noticeable osteological characters will make the description more complete.

EXTERNAL CHARACTERISTICS

Diagnostic Characters: Head short, cordiform and elevated at the vertex; occipital and temporal regions bearing flattened and grooved spines which vary in length and number; cephalic plates small and polygonal; nostrils anterior or lateral; teeth small and bluntly conical; palatine teeth lacking; body short, suborbicular, greatly depressed and usually fringed by one or two rows of spinose scales; back covered with scales which vary greatly in size and shape; scales of ventral surface, smooth and equal sized; gular folds present; tail short, usually rounded and conical; limbs short, digit moderately developed; tympanum visible or covered more or less with scales; femoral pores present; preanal pores lacking; no dorsal or caudal crest (pl. 1).

Description: The body is broad, flat and oval, usually with a lateral fringe (pl. 1). Dorsally it is covered with keeled scales which are irregular in shape and size. Ventrally the scales are small and regular, giving an imbricated appearance. Larger keeled scales cover the front of the arm and thigh. The head is short and somewhat triangular in shape with a sharp projecting margin. The projecting superciliary regions overhang a groove from the occiput to the snout, in which the eye is situated. Small subequal scales cover the top of the head and a row of bony spines, variable in length and number, are to be found on the temporal and occipital region. The projecting superciliary regions bear posteriorly short, sharp scales. Protected by bony processes and just in front of the interoccipital region, is the

median pineal eye. The lower jaw is bordered by large projecting spinous plates. The neck is short, causing transverse gular folds which often cover the auditory aperture. The pentadactyl limbs are short and about equal in length, and the digits are moderately developed, the fourth being longest. The tail is short, conical, and covered dorsally with the same sort of scales as the back. Posteriorly the ventral scales are keeled. The tympanum may be naked or covered with scales. This character varies within species, however, and is not a good basis for dividing the genus as Cope (1898) has suggested. The nostrils are conspicuous and may be either on the line joining the superciliary region with the end of the snout or above this line (pl. 2). A row of femoral pores varying in number in the different species from seven to twenty, are found in both sexes on either thigh. Those in the male are the most highly developed. The presence of enlarged postanal scales in the male is a dependable character for determining sex. Anal pores are absent. Juveniles may be distinguished by their small size and poorly developed horns.

OSTEOLOGY

The following description of the osteology was made after a study of complete skeletons as enumerated below. The generic osteology given here is largely an amplification of Cope's (1898) work.

LIST OF SKELETONS

Species	Museum number	Locality	Collector
<i>Phrynosoma douglassi douglassi</i>	Zool. Dept.	Prescott, Arizona	G. W. Treadwell
<i>Phrynosoma blainvilliei blainvilliei</i>	272	Schain's Ranch, San Jacinto Mountains, California	Charles Camp
<i>Phrynosoma blainvilliei frontale</i>	Zool. Dept.	Kern County, California	
<i>Phrynosoma platyrhinos</i>	1300	Big Creek Ranch, Humboldt County, Nevada	W. P. Taylor
<i>Phrynosoma platyrhinos</i>	1301	Pine Forest Mountains, Humboldt County, Nevada	Taylor and Richardson
<i>Phrynosoma cornutum</i>	4579		

LIST OF SKELETONS—(Continued)

Species	Museum number	Locality	Collector
<i>Anota maccallii</i>	1006	Salton Lake, Imperial County, California	F. Stephens
<i>Phrynosoma modestum</i>	Zool. Dept.	Arizona	G. W. Treadwell
<i>Sceloporus occidentalis</i>	Zool. Dept.	Near San Leandro, Alameda County, California	E. P. Rankin
<i>Dipsosaurus dorsalis</i>	1878	Colorado River at Pilot Knob, California	J. Grinnell
<i>Crotaphytus wislizeni</i>	1467	Big Creek Ranch, Humboldt County, Nevada	C. H. Richardson, Jr.

Diagnostic Characters: Parietal and supratemporal elements and often the jugal possessing spines; superciliary ridges formed by processes from the frontal and prefrontals present; postorbital spines small and short; epipterygoids short, only reaching to the petrosal; pterygoid teeth absent; sternum broad with large fontanelle; no abdominal ribs; chevron bones lacking symphyses; postischial symphysial cartilage well developed.

Description—Skull: The alveolar portion of the premaxillary is short and borders the nasal openings for a very short distance. The same openings are bordered laterally by processes arising at the middle of the maxillary elements. The nasals are distinct and form half or more of the arch over the nostrils. The unpaired frontal, narrowed anteriorly, where it articulates with the prefrontals, forms the superior arches over the orbital cavities. At the ends of the arches are small posterior, spiny processes and long, acute, anterior, superciliary processes extending forward over the orbits. The large prefrontals send processes posteriorly over the orbits forming, with the processes from the frontal, the superciliary ridges. These two processes vary in length in the different species, almost meeting in some (*Phrynosoma blainvilliei blainvilliei*, *P. b. frontale*) and widely separated in others (*P. platyrhinos*, *P. modestum*, *P. douglassi*). In *P. cornutum* they meet and partially ossify. The postfrontals are usually ossified. The lacrymals are small. The parietal overhangs the supraoccipital and supports several horns on its strong parietoquadrate arch. The number of horns is usually two with a rudimentary third between, but in *P. solare* there are four well-

developed horns. The pineal foramen is usually at the coronal suture but may pierce the parietal alone. The paraoccipital is small and partially hidden by the occipital. The supraoccipital forms the superior part of the foramen magnum and articulates anteriorly with the parietal. The occipital condyle is formed by ossified processes from the basioccipital and lateral occipital elements. The sutures of the occipital elements are lacking. The postorbitals are slender but articulate broadly with the frontals and parietals above and the supratemporals and jugals below. The supratemporals and jugals are projecting and bear spiny tuberosities except in *P. douglassi* and *P. cornutum*, where they are lacking or reduced to mere tubercles on the jugals. The quadrates are at an angle to the vertical and present an external conch only, the inner surface being convex, whereas in all other iguanids except *Eublepharis* and *Celestus*, it is concave (Cope, 1898). The short vomers are separated by a narrow hiatus which broadens between the wide, toothless palatines and the pterygoids. The palatines possess processes which run forward and outward and join the vomers in front. The palatine foramina are small and vary in shape. The short, wide pterygoids run forward from the quadrates to the basi-pterygoid processes of the sphenoid, then broaden out and articulate with the palatines. These elements are edentulate. The ectopterygoids are irregular in shape and articulate with the palatines for only a short distance. The petrosals are short and grooved inferiorly. The slender epipterygoids are peculiar in that they reach only to the petrosals. They originate just behind the ectopterygoid processes.

The Meckelian grooves may be open or partly closed by cartilage. The coronoids are situated just above the sutures between the angulars and the dentaries and articulate broadly on the interior surface of these two bones. The pleurodont teeth, one row on each dentary, are small and bluntly conical. The articulars are sometimes ossified with the surangulars.

The basihyal is wide and ossified. The rod-like anterior cornua are also ossified. The middle cornua are usually cartilaginous, very broad at the tip, and attached to the anterior

cornua at their middle and end. The posterior cornua are short and have their origin close to the middle cornua.

The orbital cavities are very large. A supratemporal opening is present in all of the species studied except *Anota maccalli*. The posterior temporal openings vary greatly in size and shape. The nasal openings may be anterior or lateral.

Vertebral Column: The procoelous vertebrae lack the zygo-sphene articulation, although there are corresponding rudimentary processes. Only the cervical vertebrae possess intercentra. There are twenty pairs of ribs, the first pair and the last four or five pairs being short. The ribs from the second to the eighth vertebra articulate by cartilage to the sternal ribs. The two sacral vertebrae are partly fused. At least six to eight caudal vertebrae possess haemal arches, the remaining being rudimentary or vestigial. The neural spines are short but show in some species a tendency to form a dorsal crest. Chevron bones are present from the fourth or fifth caudal vertebra to near the end of the tail. These bones are peculiar in the lack of a symphysis.

Pectoral Girdle: The thin suprascapulas are nearly as long as the scapulas and extend well over the back. A proscapular process is present on each scapula. The episternum is only slightly curved and extends but a short distance beyond the sternum on each side. The sternum is broad and has a large fontanelle. Two or three sternal ribs may articulate with the sternum and the xiphoid rods are connected with but one rib. In *Phrynosoma platyrhinos* the third pair of sternal ribs have their origin on the xiphoid rods and only two ribs articulate with the sternum.

Pelvic Girdle: The ilia are stout and nearly vertical in position, whereas the pubes and ischia are slender and transverse, being separated by a large ischio-pubic foramen. At the symphysis the bones are connected by cartilage. Extending posteriorly from the symphysis and dorsally toward the vertebral column, is a slender rod-like cartilage. This cartilage, although not mentioned by Cope (1898), is found in each species. Not being able to find a name for it in literature it is here termed

the postischial symphysial cartilage. In the different species it was found to vary in length and in the character of the tip. In some species (*Phrynosoma platyrhinos*, *Anota maccalli*) the tip is bifid. A tendency toward ossification was also found, the cartilage in *Phrynosoma blainvilliei blainvilliei* being ossified and that in *Anota maccalli* being partly ossified. The great difference in length and in the character of the tip, which may be found in the different species, is well illustrated in figures A and B.

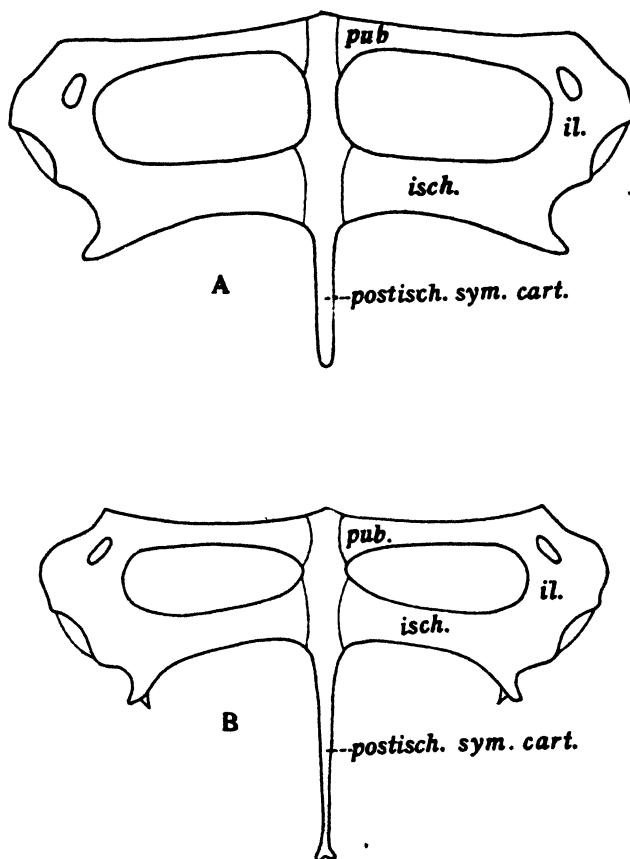


Fig. A. Pelvic girdle of *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 272). *pub.*, pubis; *il.*, ilium; *isch.*, ischium; *postisch. sym. cart.*, postischial symphysial cartilage. $\times 2$.

Fig. B. Pelvic girdle of *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1006). *pub.*, pubis; *il.*, ilium; *isch.*, ischium; *postisch. sym. cart.*, postischial symphysial cartilage. $\times 2$.

The elongation of the symphysial cartilage into a rod-like structure is found in other iguanids (*Dipsosaurus dorsalis*, *Sceloporus occidentalis*) but is developed to a less degree. The tendency to ossify appears to be peculiar to the genera *Phrynosoma* and *Anota*.

Limbs: The limbs are short but typically lacertilian. A pisiforme, ulnare, intermedium, radiale, centrale, and five carpalia compose the carpus, and five metacarpalia, the metacarpus. The tarsalia are partly united with the metatarsalia. A well-developed claw tips the digits.

INTEGUMENT

The integument of the horned lizards is much like that of other lizards except for a modification of the epidermis on the horns and the wide variation in size and shape of the dorsal scales.

On the horns and larger spinous scales the epidermis is modified into a cartilaginous cap. This cap is shed with the skin and is regenerated by the layer of epidermis which remains.

The rest of the epidermis is developed into horny plates or scales. The layer is continuous, the scales being formed by a thickening of the horny layer. The dorsal scales in this genus vary greatly in size and shape. Those of the back may be small and granular or large, keeled and tuberculated. Ventrally the scales are uniform in size and show a pavement-like arrangement. The plates of the head are usually small and regular in size but show variation in each species. Enlarged scales are found on the mandibles and periphery.

The horny epidermis is cast off periodically. This exuviation as shown by Bruner (1907), is caused by "a new growth of the stratum corneum beneath the old layer and a mechanical pushing off, of the old stratum which has been cut off from its supply of moisture and nourishment." This last part of the process is greatly aided by the growth of small prickles on the surface of the new layer. There is also a possibility that the formation of new capillaries may aid the process (Bruner, 1907). The molting process often causes the lizard a certain amount of incon-

venience. The skin usually loosens in patches and either falls off or is rubbed off. Pieces of skin two inches in diameter were found in the cage of some *P. b. blainvilliei* which were molting in September.

Hay (1892) has suggested that the ejection of blood by the horned lizard is a protection at the time of molting. This is a possibility, but it is certain that the lizard can just as easily be induced to eject blood when it is not molting. Bruner (1907), in an interesting discussion, shows the use of the large blood sinuses of the head in aiding the molting process. The increased blood pressure in the sinuses in a measure explains the ejection of blood from the eye at such a time.

Located beneath the horny layer, in the dermis, are numerous pigmented cells situated in a layer of cells containing scattered yellow pigment granules. These cells constitute the mechanism by which the lizard is enabled to change its color. In *Phrynosoma*, the color change is slow, Coues (1875) stating that the change takes place in from twenty-four to forty-eight hours. The manner in which the change in color is accomplished is not far different from that found in the chameleon and *Anolis* except that the mechanism in the latter instances is more complex. Although it is impossible to see the change take place, yet the cells involved can be easily studied under the microscope. A piece of skin from a juvenile *P. b. blainvilliei* when fixed in Erlicki's fluid and sectioned, showed large round cells filled with black pigment situated in the dermis below the scutes. In my material the pigmentation was best shown in unstained sections. The melanophores possessed many branches leading toward the epidermis, each branch dividing and redividing forming a network. In most instances the branches were filled with the black pigment. Between the melanophores and scattered through the dermis was a yellowish pigment constituting the ochrophore layer. The migration of the pigment outward or inward through these branches accounts for a dark or a light color, and is governed by the nervous system. Carleton (1903) has shown it to be the sympathetic system in the case of *Anolis*, whereas Brücke (1851) and Keller (1895) have shown it to be the cerebro-spinal

system in the chameleon. Light and heat rather than moisture probably have the most effect on the nervous system (Parker, 1904). In *Phrynosoma* light causes an inward migration of the pigment and dark, an outward migration. This is true in *Varanus*, *Agama* and several other lizards, but the opposite is true in *Anolis* (Carleton, 1903).

For the reason that the coloration varies so widely with the substratum, the color characters are omitted from the diagnoses. In the case of *P. douglassi douglassi* the distinctive features of the coloration are inserted in the key because the color characters are important in distinguishing subspecies.

On the ventral sides of the thighs, there is developed a row of glands, the so-called femoral glands. The ducts, which open on a row of enlarged scales, are formed from the stratum corneum and are filled with a mass of yellowish secretion (Shaefer, 1902). The glands are supposed to function in coition (Edwards, 1896).

REPRODUCTION

Reproduction in this genus is both oviparous and viviparous. Among the oviparous species are *Phrynosoma cornutum* and *P. blainvilliei*. The former is known to dig a hole in the earth, deposit its eggs and cover them with sand (Edwards, 1896). Several days are needed for incubation. With *P. blainvilliei*, however, the young hatch a few hours after the eggs are laid. The eggs are from fifteen to twenty millimeters in length and are covered by a tough, semi-transparent membrane. They vary in number from six to fourteen. *P. douglassi*, on the other hand, gives birth to numerous young which are able to take care of themselves a few hours after they are born (Ditmars, 1907). Young are usually produced late in the summer, although a specimen of *P. blainvilliei blainvilliei* kept in captivity laid its eggs the last of June. Specimens of the same species were seen in the act of coition in the latter part of April and in May. The period of gestation is not known.

HABITS

Phrynosoma is the most distinctly terrestrial genus of all the iguanids, in form and structure being ill adapted to climbing.

Most of the species are found in a dry, sunny climate, and usually where there is sandy soil and very little vegetation. A well known exception is that of *P. blainvilliei frontale* which occurs in the forest belt of the Coast Range in California. Such an environment provides these lizards with an abundance of insect food,—ants, beetles, flies, etc.

The horned lizard presents a fine example of protective resemblance. Wherever its home, it resembles the color of the substratum so closely that it is practically invisible except when in motion. Specimens from the white sand of the desert are very light in color, those from the black lava belt are almost black, whereas those from the vari-colored mountain districts show red and even bluish markings. How quickly a change in environment would bring about a change in color is not definitely known, although Coues (1875) states that the change takes place in from twenty-four to forty-eight hours. Several specimens of *P. blainvilliei blainvilliei* from Pasadena when kept in captivity on dark soil in the moister climate of Berkeley, on shedding their skin, showed a much darker color. This may have been due partly, however, to their being kept indoors, for Parker (1904) has proved that both light and temperature influence color change.

The most distinctive thing about horned lizards is the circlet of horns which crowns the head. Any one who has seen a horned lizard on the defensive cannot doubt the value of these horns as a protection to the animal. With its head lowered so as to receive any blow on the horns and the large scales of the back elevated, it presents a very formidable appearance. In fact, the lizard seems to depend almost entirely on the ability to frighten its enemies, for aside from the horns it has no means of defense, as it seldom attempts to bite and is not a swift runner. As most of the species are represented by large numbers of individuals, the protection appears to have been adequate.

The two greatest enemies of the horned lizard are the road runner (*Geococcyx californicus*) and the rattlesnake (*Crotalus*). A tradition existing among the Indians that a horned lizard is able to burrow its way out of a snake's stomach seems to have some foundation in fact, for rattlesnakes have been found with

the head of a horned lizard protruding through the body wall. Mr. Newhall witnessed such a phenomenon in the Yosemite Valley. Rattlesnakes have also been found with the horns of a *Phrynosoma* caught in the throat (Cope, 1898). With the coming of civilization the domestic cat becomes a formidable enemy second only to the curio collector, who has practically exterminated the horned lizards in some localities.

A *Phrynosoma* is slow and sluggish in its movements. If moving leisurely along, it drags its body on the ground, but when running stands well on its legs. When frightened, it usually tries to seek shelter in a nearby bush or buries itself in the sand. The latter operation is very interesting, for it is so widely different from the method used by other burrowing animals. The chisel-shaped head is the principal tool, the legs being used almost solely for forcing the head forward. A wriggling motion of the head and body serves to drive the head beneath the sand and soon covers the body completely with earth. A little shake of the tail flings the dirt over that appendage and the lizard becomes entirely hidden. The nostrils are kept either at the surface of the ground or near enough to the surface so that breathing is possible.

The members of this genus, like most of the *Lacertilia*, are such lovers of sunshine and heat that they are seldom found in winter or on cold or rainy days. The winter months are spent in hibernation in rodent holes or buried beneath the soil. A specimen of *P. blainvilliei blainvilliei*, plowed out on December 15, 1909, was found to be in a state of hibernation. The eyes were tightly closed and the lizard could not be induced to open them; the muscles were set, the animal often lying in a very awkward position. The breathing was slow and erratic, intervals of several minutes intervening between inspirations. The external temperature of the body was about that of the air (15° to 18° C.). Some ten minutes after placing the lizard in the sun, it showed signs of renewed energy and was ready to run at anyone's approach.

Ants, beetles, flies, and other insects form the principal diet, although Bell (1828) states that *P. douglassi* is somewhat herbivorous. Unless very hungry, live insects alone satisfy a

Phrynosoma. In fact, their eyes seem unable to distinguish an insect unless it moves, so that this may largely govern the feeding habit. On seeing its prey, a *Phrynosoma* has a habit of raising and lowering itself on its front legs much as a lizard does when sunning itself on a rock. Always when feeding it raises itself well on its legs, seemingly to avoid being bitten. The moment the insect moves, the horned lizard darts for it, catches it on the end of its viscid tongue, swallows it alive and backs off again. Why the animal is never bothered by being stung internally by the ants it eats, seems hard to explain. Certainly the lining of the mouth and stomach must be particularly adapted to withstand the poisonous sting of insects, for when stung externally, the lizard shows no little discomfiture.

The dewdrops on the vegetation may sometimes serve as the water supply. Although horned lizards go for long periods of time without water, yet they are known to drink greedily at times.

A peculiar habit of "playing possum" is often seen, the lizard remaining perfectly still, as if dead, but darting away at the first opportunity for escape.

An interesting reaction is seen in the hypnotic effect produced by rubbing the animal on top of the head and between the eyes. Under such treatment the lizard turns its head down, closes its eyes and apparently goes into a hypnotic stupor. Pinching it with a tweezers or placing it on its back, a treatment which it highly resents in a normal state, fails to awaken it. In some cases specimens remain in such a stupor for five or ten minutes. The first sign of awakening is usually evidenced by the slow opening of the eyes. This habit may be simply a "playing possum," but is probably more in the nature of hypnosis such as is produced on birds when held for a time on their backs. This phenomenon offers a field for further study.

DISTRIBUTION

Phrynosoma is distinctly a North American genus, ranging from Canada to southern Mexico and from the Mississippi to the Pacific coast. The southwestern United States and Mexico have the largest number of representatives, due probably to the

especial fitness of the soil and climate. Of nineteen recognized species and subspecies, all but eight are found in the United States, these eight being distinctly Mexican species. The Texas horned lizard, *Phrynosoma cornutum*, is perhaps the best known and most widely distributed of any of the species, being found from southern Kansas and Colorado to the Gulf of Mexico and into Mexico as far as Monterey, and from New Mexico to Arizona. Other species, as for instance *P. modestum*, have a more limited distribution.

In California and Nevada are found four representatives of the genus *Phrynosoma*, *P. blainvilliei blainvilliei*, *P. blainvilliei frontale*, *P. douglassi douglassi*, *P. platyrhinos*, and one representative of the genus *Anota*, *A. macalli* (*P. macalli*). A fifth *Phrynosoma*, *P. coronatum*, has been reported from San Diego, California (Cope, 1898). No California specimens of *P. coronatum* have been available in this study, although plenty of *Phrynosomas* from this locality were at hand. Specimens of this species in the collection at Leland Stanford Junior University were taken at San Telmo, Ensenada, San Jose del Cabo, and Santa Anita, Lower California. The majority of the known specimens are from the type locality, Cape San Lucas, Lower California. A number of specimens from San Diego County near the Mexican line (San Diego, National City, Campo, Dulzura), which were examined, are distinctly *P. blainvilliei blainvilliei*. If *P. coronatum* is found within the state it certainly is not of common occurrence. The fact that *P. coronatum* has often been used to include several species (Girard, 1858; Gentry, 1885; Ditmars, 1907) leaves the occurrence of this species in this state still in question. The two species *coronatum* and *blainvilliei blainvilliei* are separated by several distinct characters, so that they are easily identified.

Some doubt also centers around the occurrence of the pygmy horned lizard *P. douglassi douglassi* in northern California. But a single definite record, that of Charles H. Townsend (1887), from the western base of Mt. Shasta, is known. The type locality being the Des Chutes River, Oregon, its occurrence along the northern border of the state seems probable. An attempt to obtain specimens from the vicinity of Mt. Shasta failed, as did

also one to secure them from across the line in Oregon, where it was stated they had been seen. Several people living at Sisson, a town on the southwestern base of the mountain, stated that they had never seen a horned lizard in that locality. No distinctly California specimens being at hand, the discussion of this species has necessarily been abbreviated.

The type locality of *Phrynosoma blainvilliei* was originally given as "California" without specification of locality. Since the division of the species into *P. blainvilliei* and *P. frontale* by Dr. Van Denburgh (1903), the distribution of *P. blainvilliei* should be restricted to southern California. An examination of a large number of specimens of these two species showed an intergradation of the diagnostic characters used by Van Denburgh. This fact, as well as others, indicate that these lizards belong to races rather than species. Cope (1898) has already suggested this. The two have therefore been reduced to subspecific rank and are referred to as *Phrynosoma blainvilliei blainvilliei* and *Phrynosoma blainvilliei frontale*. A discussion of the intergradation and the reasons for the reduction can be found on page 35.

Blainville's horned lizard, *Phrynosoma blainvilliei blainvilliei*, is the common horned lizard of southern California, being found on the coastal slope from Los Angeles County southward to the Mexican line. Specimens from San Diego County are considered most typical. An intergradation with *Phrynosoma blainvilliei frontale* takes place in northern Los Angeles County (see page 35).

The California horned lizard, *P. blainvilliei frontale*, is found principally in the San Joaquin basin, although there are many records of its occurrence in the counties along the coast from San Mateo County southward. The most northern record is from Colfax, Placer County, and the most southern of individuals showing distinctly *P. b. frontale* characteristics, from Matilija, Ventura County. The type specimen in the collection of the Leland Stanford Junior University is from Bear Valley, San Benito County, California.

The three remaining species are limited to desert regions. *P. platyrhinos*, the desert horned lizard, occurs abundantly in

Nevada, the Mojave Desert, and the northern part of the Colorado Desert of California. There are also records from Arizona. The hottest and most arid parts of the deserts seem to be the most attractive for this lizard. The type specimen was obtained from the basin of Great Salt Lake.

A single specimen of a horned lizard collected in Death Valley, Inyo County, California, was described by Cope (1896) as a new species, *Anota calidiarum* (*Phrynosoma calidiarum*). The type being the only specimen known, and the differences from *P. platyrhinos* being very slight, there is some doubt as to the validity of the species.

The flat-tailed horned lizard, *Anota maccalli*, the other desert species, is rare and found only on the Colorado Desert of Imperial County, California, the Gila Desert, and Sonora, Mexico. The type specimen was taken between Vallecito and Camp Yuma, about 160 miles from San Diego. Van Denburgh (1897) gives this as the only California record of *A. maccalli*, the other three specimens belonging to the U. S. National Museum being from Fort Yuma, Arizona. Of this rare species there are at present in the Museum of Vertebrate Zoology of the University of California eight specimens, four from Mecca, three from Salton Lake, and one from Coyote Well. Several specimens of *P. platyrhinos* were taken at Mecca at the same time that *Anota maccalli* was collected, which would show an overlapping of the areas of distribution of the two species at this point.

Another overlapping of areas of distribution is to be noticed in the case of *Phrynosoma blainvilliei frontale* and *P. platyrhinos*, for specimens of both species have been taken in Walker Pass, along the Kern River near Chimney Creek, and on the west slope of the divide, at an altitude of 5500 feet, in Kern County, by members of the Mt. Whitney Expedition of 1911 of the Museum of Vertebrate Zoology of the University of California. Doubtless the same intermingling of species takes place at other points in the Sierras, for, although this range of mountains forms the western boundary for *P. platyrhinos* and the eastern boundary for *P. blainvilliei frontale*, it in no way forms an insurmountable barrier for these lizards.

There are no records of any species of *Phrynosoma* from the islands off the California coast, although some of the other lizards, as, for example, *Sceloporus* and *Uta*, are abundant there. *P. cerroense* is found only on Cerros Island off the coast of Lower California.

The appended map (pl. 8) shows clearly the distribution of the five species of horned lizards inhabiting California and Nevada. In the preparation of the map only reliable records were used. In no case were records incorporated where the subspecies could not be differentiated.

As the map shows, each species inhabits a rather well defined region and there is little overlapping of areas of distribution. Generally speaking, the distribution of these species conforms fairly well to the faunal areas proposed by Van Denburgh (1897). According to his analysis, the Colorado and Mohave deserts comprise the Desert Fauna; the southern end of the state, comprising San Diego (including what is now Imperial), Orange, Riverside, San Bernardino, and Los Angeles counties, constitutes the San Diego region; the western slope of the Sierra Nevadas westward to the ocean, the Californian; a strip along the coast, north of Monterey, the Pacific; and the mountainous region of the Sierra Nevada, the Sierra Nevadan. Thus, *P. platyrhinos* and *A. maccalli* would belong to the desert fauna, *P. b. blainvilliei* to the San Diegan, *P. b. frontale* to the Californian, Pacific, and possibly the Sierra Nevadan, and *P. d. douglassi* to the Pacific and Sierra Nevadan.

As might be expected, the desert species, *Phrynosoma platyrhinos* and *Anota maccalli* show some special modifications which may be related to their environment. The most noticeable one is the reduction of the enlarged keeled scales of the back. Compared with *P. b. blainvilliei* and *P. b. frontale*, these species present a rather smooth skin made up of small scales of unequal sizes and irregular distribution with the spiny scales reduced in size. In the ear opening we find the most characteristic modification, a characteristic which Cope (1898) has used in dividing the species into the genera *Phrynosoma* and *Anota*. In *A. maccalli* we find the ear opening entirely closed and in *P. platyrhinos* it is covered completely or partially by

scales. In the former, even a depression is scarcely discernible. The latter, however, shows clearly the location of the opening. That this unusual modification is some particular adaptation to environment would seem to be proved by its prevalence among all truly desert species of horned lizards. None of the other iguanids except *Holbrookia* show this adaptation, however. A slight reduction in size in *P. platyrhinos* and a greater reduction for *A. macCalli* is also to be noted in this connection.

KEY TO GENERA AND SPECIES

[Based in part on that of Van Denburgh (1907)]

- A. Horns flattened and grooved; one or two rows of peripheral spines; tail rounded; supratemporal openings present *Phrynosoma*
 - a. Nostrils on the line joining the superciliary ridge with the end of the snout.
 - b. One row of peripheral spines; occipital horns rudimentary; no rows of enlarged gular scales *P. douglassi*
 - c. Size small (70-90 mm.); horns mere tubercles; snout blunt; coloration inconspicuous *P. douglassi douglassi*
 - bb. Two rows of peripheral spines; occipital horns well developed; three rows of enlarged gular scales *P. blainvillici*
 - d. Head shields convex and almost smooth, centrally located ones largest *P. blainvillici blainvillici*
 - dd. Head shields flat, with numerous ridges and granulations, size uniform *P. blainvillici frontale*
 - aa. Nostrils above the line joining the superciliary ridge with the end of the snout.
 - e. Horns short (4-8 mm.); one row of peripheral spines; six to twelve femoral pores *P. platyrhinos*
 - AA. Horns long (8-12 mm.), smooth and conical; three rows of closely-set, peripheral spines; tail flat; supratemporal openings absent *Anota*
 - f. Nostrils anterior; sixteen to twenty femoral pores *A. macCalli*

Phrynosoma douglassi douglassi (Bell) Stejneger

Pigmy Horned Lizard

Agama Douglassi Bell (1828), pp. 105-107, 1 pl.

Phrynosoma douglassi Girard (1858), pp. 361-362, pl. 7, figs. 6-10.

Tapaya douglassi Girard (1858), pp. 397-399, pl. 21, figs. 1-5.

Phrynosoma douglassi pygmaea Yarrow (1882), p. 448

EXTERNAL CHARACTERISTICS

Diagnostic Characters: Head broader than long; nostrils at the end of the superciliary ridge; occipital horns very short, being in some cases mere tubercles; supratemporal horns projecting farther posteriorly than the occipital; head plates irregular in size and shape, and usually convex and granulated; sublabials not much larger than infralabials, the last three or four

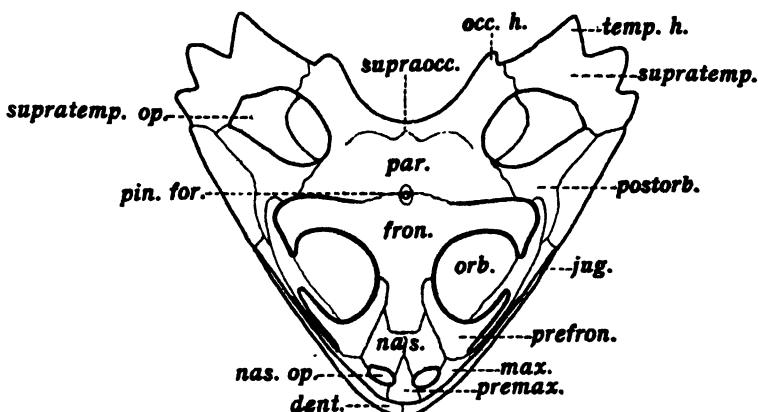


Fig. C. Skull of *Phrynosoma douglassi douglassi* (Zool. Dept.). *dent.*, dentary; *fron.*, frontal; *jug.*, jugal; *max.*, maxillary; *nas.*, nasal; *nasal op.*, nasal opening; *occ. h.*, occipital horn; *orb.*, orbit; *par.*, parietal; *pin. for.*, pineal foramen; *prefron.*, prefrontal; *premax.*, premaxillary; *postorb.*, postorbital; *supraocc.*, supraoccipital; *supratemp.*, supratemporal; *supratemp. op.*, supratemporal opening; *temp. h.*, temporal horn. $\times 2$.

enlarged and pointed; a conical rictal scale present; gular scales small and equal in size; body with one row of peripheral spines; back and tail with several rows of large, keeled, spiny scales set among smaller scales and granules; abdominal scales small and smooth; tail slender and rounded toward tip; tympanum usually visible but sometimes covered with scales; femoral pores in long series almost meeting medially.

Description: The horns are very rudimentary, reduced to blunt, conical tubercles, and flattened and grooved, those of the supratemporal elements projecting beyond those of the occipital region (pl. 3, fig. 7). The two occipital spines are widely separated at the base. An enlarged scale alone gives evidence of

an interoccipital. A series of four or five temporal horns are found on each side. One row of peripheral spines fringes the small body. The tail is enlarged near its base and then narrows suddenly into a short cylindrical part. It is fringed by a row of conical scales and is covered dorsally and ventrally by the same sort of scales as are found on the back and belly. The nostrils are situated on the line joining the superciliary ridge with the end of the snout. The muzzle is almost vertical. The gular scales are of equal size (pl. 3, fig. 8). The head is obtusely triangular, broader than long, and the superciliary region is strongly marked. Scales of the row on the margin of the superciliary ridge are enlarged, the central one acting as a keystone. The infralabial scales are larger than the supralabials, the last four to six being enlarged and pointed, forming a row of subrictals. At the rictus is situated an enlarged, conical scale. The limbs are short. The enlarged dorsal scales are arranged in several rows but are not conspicuous. They are not surrounded at their base by a rosette. The abdominal scales are smooth and acute. Long series (usually sixteen) of conspicuous femoral pores approach the median line invading the preanal region. Males usually have enlarged postanal plates. See table of measurements for dimensions and proportions of the lizard.

The coloration varies greatly, the commonest being ashy to brown with several rows of dark blotches. The neck patches are narrow and widely separated (pl. 1, fig. 1). The tail and limbs are obscurely cross-banded. A faint, central white line runs from the occiput to the tail. The ventral surface is usually spotted as is also the gular region. For general color pattern see plate 3, figure 7.

OSTEOLOGY

Diagnostic Characters: Horns of occipital region rudimentary and widely separated; supratemporal horns extending posteriorly to them; nasals with short, obtuse processes over nostrils; spines on jugal elements lacking; postorbitals with broad articulating processes turned at right angles to each other; quadrates long with deep conchs; the epityrgoids run along the petrosal

for two millimeters; postischial symphysial cartilage short (3 mm.) and not bifid.

Description: The alveolar portion of the premaxillary (*premax.*, fig. A) does not border the nostrils (*nas. op.*). The nasals (*nas.*) have a short obtuse process directly over the nasal opening. The superciliary processes from the frontal (*fron.*) are short and sharp; those from the prefrontals (*prefron.*) end in a sharp point above the middle of the orbit (*orb.*). The two rudimentary occipital horns (*occ. h.*) are widely separated. An interoccipital spine is represented by an enlarged, obtusely pointed scale. The horns on each supratemporal element (*supratemp. h.*) are three in number and the posterior ones extend farther back than the occipital horns. The pineal foramen (*pin. for.*) is at the coronal suture. The postorbitals (*postorb.*) have very broad articulations with the supratemporals (*supratemp.*) and jugals (*jug.*) and less broad ones with the frontal and parietal (*par.*). The broad processes for the latter articulations are turned at right angles to the processes for articulation with the former. There are no spinous processes on the jugals. The nearly vertical quadrates are long and narrow with deep conchs. The palatine foramen is long (3-4 mm.) and narrow. The upper part of the epipterygoids runs along the petrosal for about two millimeters.

All of the elements making up the inferior mandible are thick and heavy. Meckel's groove is short. Cope (1898) states that the surangular is ossified to the articular in this species, but the writer's specimen showed a well-defined suture.

The supratemporal openings (*supratemp. op.*) are large. The nasal apertures (*nas. op.*) are lateral (pl. 2, fig. 2).

There is no evidence of a dorsal crest, the neural spines being very nearly equal in size. The transverse processes of the caudal vertebrae are short and are absent on the last five or six vertebrae. The first pair is only a little shorter than the second and third pair. Three sternal ribs articulate with the sternum (pl. 8, fig. 17). The postischial symphysial cartilage is three millimeters long and is not bifid.

Phrynosoma douglassi, which is the smallest of the horned lizards, has three recognized subspecies, *P. douglassi douglassi*

(*P. douglassi pygmaea*), *P. douglassi hernandesi* and *P. douglassi ornatissimum*. The first is found only in the North Pacific district, the second only through the central district, the Rocky Mountains and Great Basin, and the third, the desert species, only on the deserts east of the Sierra Nevada. *P. douglassi douglassi* is much smaller than the other subspecies and may be distinguished also by its very blunt snout, its very rudimentary horns and its inconspicuous color. Cope (1898) suggests that the characters define races which do not seem to be sufficiently distinct to represent subspecies.

The first description of this species was made by Bell (1828) from a specimen collected in Washington by H. W. Henshaw. Yarrow (1882, 1887) gave specimens from the same locality the subspecific name of *pygmaea* on account of their small size. This name, however, had to give way to that of *douglassi* when the subspecies were fully worked out by Stejneger (1890) and Cope (1898).

HABITS

Bell (1828) states that these horned lizards are always found in the immediate vicinity of water. If this be true, *P. douglassi douglassi* is different from other members of the genus, for most *Phrynosomas* depend upon the drops of dew on the vegetation for their water. It is also stated by the same author that this subspecies lives partly on the surrounding vegetation. This would seem another exception to the general rule, for all the species studied were found to be strictly insectivorous. These two observations need verification.

The protective coloration assumed by this species is very interesting. All shades and colors from the obscure gray skin of *P. douglassi douglassi* to the brightly spotted skin of *P. douglassi ornatissimum* are to be found. Indeed the character of the coloration is so modified by the environment that it is found constant enough to act as one of the characters for distinguishing subspecies. The large *P. douglassi ornatissimum* resembles the vari-colored rocks of the Painted Desert of Arizona where it is found, whereas *P. douglassi douglassi* resembles the gray uncolored soil on which it occurs.

DISTRIBUTION

P. douglassi douglassi is of common occurrence in Washington, Oregon, Idaho and Utah. Bell (1828) in first describing it, gave its distribution as the banks of the Columbia River. C. H. Townsend (1887) records it from the western base (quoted in Van Denburgh, 1897, as northern) of Mt. Shasta, California. No other record of its occurrence in California is known, but it seems possible that it may range south from Oregon into the northern part of the state. It has been recorded from the following localities: Mt. Shasta, Shasta County, California; Des Chutes River, Grants, Willamette Valley, and between Warner's and Goose lakes, Oregon; Fort Steilacoom, Fort Walla Walla, North Yakima, and Spokane, Washington; near head of Birch Creek, desert at sink of Big Lost River, Clear Water River, Lewiston, Arco, American Falls, Snake River, Pocatella, Shoshone, Conaut, Cottonwood Creek, and Big Butte, Idaho.

Measurements: Measurements in the tables are in millimeters and were taken as follows:

Total length: from tip of snout to tip of tail.

Width of head: greatest width, across parietal region from tip to tip of temporal horns.

Snout to ear: from tip of snout to auricular aperture.

Occipital horns: from junction of horns to occipital bone to tip of horn.

Fore limb: from axilla to tip of longest toe on right fore limb.

Hind limb: from axilla to tip of longest toe on right hind limb.

Base of fifth to end of fourth toe: from base of fifth to tip of fourth toe on right hind limb.

TABLE OF MEASUREMENTS

Museum number	Sex	Locality	Phrynosoma douglassi douglassi				Ratios to total length				Ratios to width of head					
			Total length	Length of tail	Width of head	Length of limb from snout to ear	Length of limb from snout to eye	Width of head	Length of limb from snout to ear	Length of limb from snout to eye	Width of head	Length of limb from snout to ear	Length of limb from snout to eye	Width of head		
2842	♀	Arco, Alturas Co., Idaho	85.0	28.0	17.0	14.0	1.5	26.0	34.0	10.0	33.5	20.0	16.5	40.0	8.25	88.5
2816	♀	Cottonwood Cr., Cassia Co., Idaho	83.0	25.5	16.5	12.5	1.0	25.0	31.5	10.0	31.0	19.9	15.0	38.0	7.58	60.5
2801	♀	Conant, Cassia Co., Idaho	89.0	29.0	17.5	14.0	1.5	26.0	33.0	10.0	33.0	19.7	15.7	37.0	8.00	86.0
..... ¹	♀	Spokane, Washington	93.0	32.0	21.0	15.0	3.0	31.0	42.0	13.0	34.4	22.3	16.1	45.2	7.15	43.0
1951	♂	North Yakima, Washington	72.0	27.0	12.5	10.5	0.5	21.0	29.0	9.0	37.4	17.3	14.6	40.5	8.40	47.5
2840	♂	Arco, Alturas Co., Idaho	71.0	25.0	14.0	10.5	1.0	21.0	29.0	9.0	35.2	19.7	14.8	40.8	7.50	71.5
1944	♂	Pocatello, Idaho	69.0	24.0	14.0	10.5	1.0	21.0	29.0	9.5	34.8	20.1	15.2	42.0	7.50	71.5
Average of males			87.5	28.6	18.0	13.8	1.7	27.0	35.1	10.7	32.9	20.4	15.8	40.0	7.74	69.0
Average of females			70.6	28.0	13.5	10.5	0.8	21.0	29.0	9.1	35.8	19.0	14.8	41.1	7.80	63.5
Average			79.0	28.3	15.7	12.1	1.2	24.0	32.0	9.0	34.3	19.7	15.3	40.5	7.77	66.2

¹ In the collection of the Department of Zoology of the University of California. The other specimens are in the collection of the Leland Stanford Junior University.

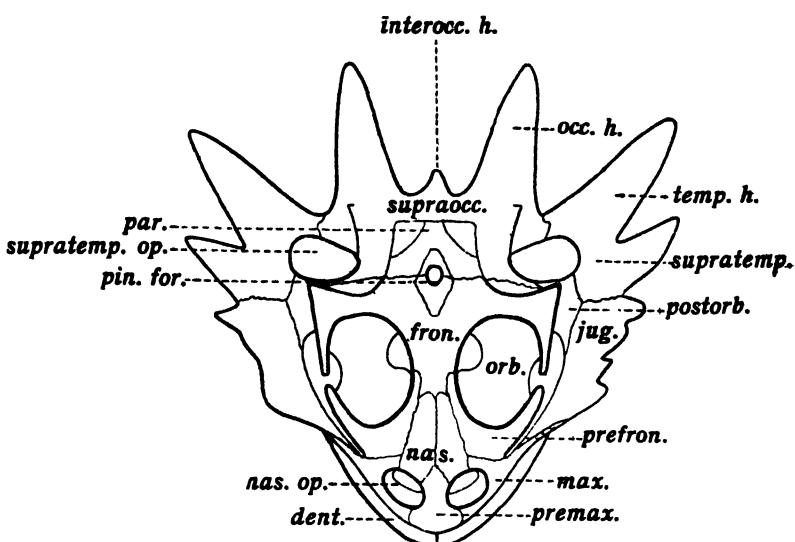
Phrynosoma blainvilliei blainvilliei (Gray) Bryant**Blainville's Horned Lizard***Agama coronatum* Blainville (1835), p. 284, pl. 25, fig. 1.*Phrynosoma coronata*, Dumeril and Bibron (1837), p. 318.*Batrachosoma coronatum* Girard (1858), pp. 400-402, pl. 20, figs. 10-13.*Phrynosoma Blainvillii* Gray (1839), p. 96, pl. 29, fig. 1.

Fig. D. Skull of *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 272). *dent.*, dentary; *fron.*, frontal; *jug.*, jugal; *interocc. h.*, interoccipital horn; *max.*, maxillary; *nas.*, nasal; *nas. op.*, nasal opening; *occ. h.*, occipital horn; *orb.*, orbit; *par.*, parietal; *pin. for.*, pineal foramen; *prefron.*, prefrontal; *premax.*, premaxillary; *postorb.*, postorbital; *supraocc.*, supraoccipital; *supratemp.*, supratemporal; *supratemp. op.*, supratemporal opening; *temp. h.*, temporal horn. $\times 2$.

EXTERNAL CHARACTERISTICS

Diagnostic Characters: Head short and thick; snout not separated from frontal region by a prominent angle; nostrils on the line joining the supraciliary ridges with the end of the snout; occipital horns large, flattened and grooved; interoccipital horn small (1-2 mm.), supratemporal horns three to six on each side; head plates convex and almost smooth; sublabials spinose, five to six in number and continued posteriorly with smaller plates;

below the rictus a large broad infrarictal spine followed by a smaller conical one; enlarged gular scales, in three or more double rows; peripheral spines in two widely separated rows, the upper being the largest; back and tail covered with large scattered scales which are strongly keeled and tubercular, set among smaller scales and granules; ventral scales smooth; tail conical and fringed by a row of widely separated trihedral spines; tympanum not covered by scales; femoral pores in long series (12-18).

Description: The two occipital horns are strongly developed, flattened and grooved (pl. 4, fig. 9). A small (1-2 mm.) inter-occipital spine is present. The horns of the occipital region are raised above those of the temporal region. The nostrils are on the lines joining the superciliary ridge with the end of the snout which is not separated from the frontal region by a prominent angle. There are two widely separated rows of peripheral spines, the upper being the largest. Three or more longitudinal rows of pointed gular scales, the inner rows being the smallest, are to be found on each side of the gular region. These rows form an apex at the front of the jaw and continue posteriorly onto the gular folds (pl. 4, fig. 10). The head shields are convex and almost smooth, some of the centrally situated ones being the largest. Four or more bony tuberosities are to be found on the parietal region in front of the occipital spines. The temporal horns are four to six in number on each side. The posterior one is much the largest. The postorbital spine is well developed. The temporal scales are ridged in the general direction of the temporal horns. A series of five or six large sublabial spines is continued posteriorly by several smaller scales. At the corner of the mouth is a large, flattened scale below which is a large and very broad infrarictal spine followed by a smaller conical one.

The back is covered with large, scattered scales which are somewhat elevated, keeled and tubercular and set among smaller scales and granules (pl. 4, fig. 9). The ventral scales are smooth and of equal size. Dorsally the tail is covered with the same sort of scales as those found on the back; ventrally the small equal-sized scales become keeled on the terminal portion. A

small group of conical spines is found on the tail just behind the thigh. This group of spines is situated just below the beginning of the one row of widely separated lateral spines which fringe the tail. The scales on the anterior surface of the limbs are large, pointed, and keeled. The tympanum is not covered with scales. A long series (12-18) of femoral pores is present on the anterior surface of the thigh (pl. 4, fig. 10). The males have enlarged postanal plates. See table of measurements for dimensions and proportions of the lizard.

The color above is gray to brownish with undulate cross bands or irregular blotches of dark brown. Two large, dark brown patches are situated on each side of the neck, the upper edge being the darker. These patches give the appearance of shadows made by the horns (pl. 1, fig. 1; pl. 4, fig. 9). The head scales are usually yellowish or slate and the horns reddish or brown. Below the color is yellowish to white and usually irregularly spotted with small dark patches (pl. 4, fig. 10). Young specimens are usually more brightly colored and show more distinct markings. For general color pattern see plate 4, figure 9.

OSTEOLOGY

Diagnostic Characters: Horns of occipital region well developed, flattened and grooved; interoccipital horn small and sharp; supratemporal horns usually two on each element, the posterior the largest; jugals presenting three or four tuberosities each; postorbitals well developed; four bony tuberosities present in front of the occipital horns on the parietal region; mandibles forming acute angles at their symphyses; lower mandible with no bony tuberosities; quadrates long (6 mm.); coronoids heavy; basipterygoid processes strong; six or seven enlarged neural spines showing evidence of a rudimentary dorsal crest; xiphoid rods widely separated from third pair of sternal ribs; post temporal openings large.

Description: The alveolar portion of the premaxillary (*premax.*, fig. D) borders the nostrils (*nas. op.*) for a short distance. The nasals (*nas.*) form but part of the arches over the same openings. The superciliary processes of the prefrontals (*prefron.*) are but little longer than those of the frontal (*fron.*) and

do not meet the latter. The two occipital horns (*occ. h.*) are large, flattened and grooved. The interoccipital horn (*interocc. h.*) is small and sharp. Four bony tuberosities are found on the parietal region (*par.*) just in front of the occipital horns. The pineal foramen (*pin. for.*) pierces the parietal only, in the specimen examined. Usually but two horns are developed on each of the supratemporal elements (*supratemp. h.*), but there may be a smaller third one. The posterior ones on each side are always the largest. Each jugal (*jug.*) presents three or four tuberosities. The postorbital (*postorb.*) ridges of the frontal possess small tuberosities directly back of the orbit. The quadrates are long (5-7 mm.). The epipterygoids just reach the petrosal.

The Meckelian groove is open posteriorly. The coronoids are heavy. The surangular is not completely ossified to the articular. There are no bony tuberosities on the lower mandible (pl. 2, fig. 4).

Six or seven enlarged neural spines show evidence of a rudimentary dorsal crest. The transverse processes of the sacral vertebrae are heavy and strong, those of the first caudal vertebrae about as long as those of the second and third. The chevron bones are well developed. The xiphoid rods are widely separated from the three sternal ribs (pl. 8, fig. 18). The ossified postischial symphyseal cartilage is four to five millimeters long and is not bifid (fig. A).

The name *P. coronatum* has sometimes been used to include two species (Boulenger, 1885; Gentry, 1885; Ditmars, 1907), one of which presents at least two distinct subspecies. Although in general outward appearance *P. blainvilliei* and *P. coronatum* are much alike, yet the latter is easily distinguished by its long, sharp, occipital horns, its well-developed interoccipital, its four well-developed supratemporal horns and by the lack of a conical spine behind the infrarictal, the presence of two rows of peripheral spines on the tail, and the dark-colored, equal-sized head plates which are outlined with light-colored lines at the sutures.

P. coronatum is distinctly a Lower California species, yet it ranges far north of its type locality, Cape St. Lucas, Lower California, and has even been reported from San Diego (Cope,

1898). As has already been noted (p. 18), its occurrence so far north, however, is somewhat doubtful and certainly rare.

HABITS

P. blainvilliei blainvilliei, next to *P. cornutum*, the Texas horned lizard, is perhaps the best known member of the genus, for this is the one largely used by the curio dealer. Then, too, it is easily domesticated and can be kept in captivity for a long time, if properly fed.

It is from this species that most of the knowledge in regard to the ejection of blood from the eyes has been derived. This habit was early discovered by the Mexicans, who called this lizard the "sacred toad" because it wept tears of blood. Nearly every small boy in the region where this species is common knows of the phenomenon and can usually cite definite instances when a horned lizard has "spit blood."

The writer has several times witnessed this strange habit. The first indication of the phenomenon to be noticed is a swelling of the eyelids to two or three times their natural size, so that they bulge from the head. During this procedure the eyes are tightly closed and the animal remains perfectly quiet. Suddenly a fine stream of blood shoots up from beneath the upper eyelid, usually with force enough to send it six or eight inches before dividing into fine drops. In one instance the blood was squirted about fifteen inches. Sometimes the blood is ejected so suddenly that the first indication of it is its contact with the observer's skin or a few drops left on the eye of the lizard. Dr. Hay (1892) states that in a specimen of *P. blainvilliei frontale* the phenomenon was repeated several times. In the writer's experience a specimen could not be induced to eject blood again from the same eye, at least, until some time had elapsed.

Miss Myrtle Johnson, carrying on some experiments with *Phrynosoma blainvilliei blainvilliei* at San Diego during the early part of July, 1911, induced a specimen to eject blood. The first indication noticed was the presence of blood on the hand. A juvenile not more than one and one-half inches long was brought to her by a small boy with the report that it had "spit blood." Circumstantial evidence in the form of blood on the eye seemed

to prove the boy's statement. If the fact can be verified that a juvenile can eject blood as well as an adult, the theory that it is a habit only used during the breeding season would seem to be disproved.

A few generalizations on this habit may be of interest. Although cases are not rare where the lizard ejects blood on being caught, yet in two cases when success attended the experiment, the lizards were awakened from the stupor brought on by the night. The eyelids, on being sectioned, were found to be highly vascular and to contain large blood sinuses. Especially was this true of the upper lids. No duct was found and it seems probable that the blood is forced out by the rupturing of a vessel. H. L. Bruner (1907), in a paper on the "Cephalic Veins and Sinuses of Reptiles," gives the best explanation yet advanced. He says, in speaking of *Phrynosoma*, "It is not improbable in this case that the mechanism for elevating the blood-pressure is used as a fright mechanism. Such a function, however, is not sufficient to explain the wide distribution of the mechanism. On the contrary, it is probable that the flooding of the cephalic sinuses for frightening enemies is at best only a secondary use which has been acquired by relatively few forms."

These lizards show great aversion to dogs. When angered by one, the lizard presents a very bristling appearance by elevating the enlarged scales of the back, opens its mouth and gives a hissing noise by quickly expelling the air from the lungs. At such times it stands well upon its legs, and puffs itself up to nearly twice its natural size. A *blainvilliei*, when first caught, often hisses at any moving object.

At the sight of a snake, however, instead of standing its ground and attempting to frighten the intruder, it generally seeks to escape. A small California ring-neck snake (*Diadophis amabilis*) when placed in a cage containing several of these lizards, created no little excitement. When the excitement had somewhat quieted down, two of the lizards became courageous enough to take a nip at its tail. This would in a measure seem to corroborate the statement that has been made that these animals attack a snake when cornered.

The food consists principally of ants, although the smaller

beetles and flies seem to be eaten with relish. Even a large Jerusalem cricket does not daunt one of these lizards, for it seizes it by the head and, not being able to swallow it directly, either rubs it to pieces on the earth or works itself around it much as a snake does. A few drops of milk placed in the cage seemed to be enjoyed by old and young alike.

DISTRIBUTION

Dr. Van Denburgh (1894) placed the horned lizards inhabiting central California in a distinct species, under the name of *Phrynosoma frontalis*, basing his division on the character of the head scales. In a later work (Van Denburgh, 1897) the same division is made, using the specific name *frontale*. In this work he suggests that an intergradation between the two species *P. blainvilliei* and *P. frontale* may take place in Santa Barbara or Ventura counties. The evidence at hand would seem to show that this intergradation takes place in Los Angeles County. All Santa Barbara and Ventura County specimens examined have equal sized, ridged and granulated head plates, showing them to be *P. frontale* and all from San Bernardino, Riverside, Orange and San Diego counties have smooth, convex head plates, the centrally located ones being the largest, characters of *P. blainvilliei*, whereas specimens from Los Angeles County show characteristics of both, the head plates being unequal in size and showing a tendency to be ridged and granulated. The fact that there is an intergradation in a rather well defined locality, tends to prove that the two species are merely geographical subspecies.

All of the other species of horned lizards, at least in the United States, have well-defined characters. Since these two forms, *P. blainvilliei* and *P. frontale*, are separated by such subordinate characters and show an intergradation, they have been reduced to subspecific rank. Further study may show that the intergrades have enough distinct characters and occupy such a definite locality that they too can be described as subspecies. Sufficient material is not at hand to justify such a division here.

P. blainvilliei blainvilliei occurs only on the coastal slope between San Diego and Pasadena. It is especially common in the valleys at the base of the San Gabriel, San Bernardino and San

Jacinto mountains. In some places, as Cajon Pass, San Bernardino County, and Warner's Pass, San Diego County, it crosses the divide onto the desert. In altitude it ranges from just above sea-level to over five thousand feet. In a series of some thirty specimens from the San Jacinto Mountains, from localities ranging in altitude from 1500 to 5000 feet, no differentiation according to altitude could be discovered. The color of the soil, however, could readily be determined by the coloration of the lizards.

A study was made of specimens collected at the following localities: Campo, Dulzura, Warner's Pass, National City, San Diego, and Escondido, in San Diego County; Oak Springs, Schain's Ranch, Fuller's Mill, Poppet Flat, Vandeventer Flat, Kenworthy, and Hall Grade, near Cabazon, in the San Jacinto Mountains, and Cabazon, Banning, and Riverside, in Riverside County; Santa Ana, in Orange County; Sanvenoska, Clarke's Ranch, and Santa Ana Cañon, in the San Bernardino Mountains, and Colton, Grapeland, and Ontario, in San Bernardino County; and Claremont, mouth of San Gabriel Cañon, and Sierra Madre, in Los Angeles County.

A list of specimens showing an intergradation with *P. blainvillei frontale* follows:

LIST OF SPECIMENS SHOWING AN INTERGRADATION BETWEEN *Phrynosoma blainvillei blainvillei* AND *Phrynosoma blainvillei frontale*

Museum number	Sex	Locality	Collector
851	♀	Pasadena, Los Angeles County, California	J. Grinnell
852	♀	Aroyo Seco, Pasadena, California	J. Grinnell
853	♀	Pasadena, Los Angeles County, California	J. Grinnell
2412	♀	Pasadena, Los Angeles County, California	H. L. Bryant
2413	♂ jun.	Pasadena, Los Angeles County, California	H. L. Bryant
2478	♂ jun.	East Pasadena, Los Angeles County, California	H. L. Bryant
2479	♂ jun.	East Pasadena, Los Angeles County, California	H. L. Bryant
2480	♀	East Pasadena, Los Angeles County, California	F. Davis
	♀	East Pasadena, Los Angeles County, California	R. N. Bryant
	♀ jun.	East Pasadena, Los Angeles County, California	R. N. Bryant
	♂	Milliard's Cañon, near Pasadena, Los Angeles County, California	R. N. Bryant
855	♂	Tuhunga Valley, Los Angeles County, California	J. Grinnell
	♂	Sierra Madre, Los Angeles County, California	C. Camp

V. TABLE OF MEASUREMENTS
Phrynosoma blainvilliei blainvilliei

Museum number	Sex	Locality	Total length								Ratios to total length				Ratios to width of head				Tail		Hind limb		Snout to ear		Width of head		Length of horns		Snout to ear	
			Length of tail		Width of head		Snout to ear		Length of occ. horns		Length of fore limb		Length of hind limb		Base of 5th to end of 4th toe		Tail		Hind limb		Snout to ear		Width of head		Length of horns		Snout to ear			
24	♂	Reeche Cañon, near Colton, Calif.	134.0	48.0	30.0	19.0	10.5	40.0	52.0	16.0	35.5	38.8	14.1	22.4	35.0	63.3														
102	♂	Banning, Riverside Co., Calif.	132.0	41.0	30.0	18.0	11.0	41.0	52.0	15.0	31.5	39.4	13.7	22.5	36.6	60.0														
274	♂	Shains Ranch, San Jacinto Mts., Calif.	120.0	37.0	26.0	15.0	9.0	40.0	51.0	17.0	31.0	42.5	12.5	21.5	34.6	57.8														
856	♂	San Gabriel Cañon, Azusa, Calif.	133.0	45.0	32.0	18.0	13.0	41.0	51.0	17.0	33.5	38.4	13.5	24.0	35.3	56.5														
382	♂	Dulzura, San Diego Co., Calif.	113.0	42.0	25.5	16.0	7.0	36.0	46.0	14.0	36.5	40.7	14.1	22.5	27.5	62.7														
59	♀	Reeche Cañon, near Colton, Calif.	122.0	38.0	31.0	18.0	11.0	37.0	49.0	14.0	31.5	40.1	14.8	25.4	35.5	58.0														
275	♀	Shains Ranch, San Jacinto Mts., Calif.	118.0	35.0	26.0	16.0	9.5	37.0	46.0	16.0	35.0	39.0	13.6	22.0	36.6	61.5														
872	♀	Escondido, San Diego Co., Calif.	124.0	36.0	27.5	17.0	9.0	41.0	52.0	17.0	29.0	42.0	13.7	22.2	32.7	61.9														
1041	♀	Warner Pass, San Diego Co., Calif.	144.0	48.0	31.5	17.0	11.0	45.0	55.0	17.0	33.0	38.1	11.8	21.9	34.9	54.0														
..... ¹	♀	San Diego, Calif.	148.0	47.0	33.0	19.0	12.0	45.0	54.0	17.0	31.5	36.5	12.8	22.3	36.4	57.5														
		Average of males	126.4	42.6	28.7	17.2	10.1	39.6	50.4	15.8	33.6	39.9	13.5	22.5	33.8	60.0														
		Average of females	131.2	40.8	29.8	17.4	10.5	41.0	51.2	16.2	32.0	39.1	13.2	22.7	35.2	62.5														
		Average	128.8	41.7	29.2	17.3	10.3	40.3	50.8	16.0	32.8	39.5	13.3	22.6	34.0	61.2														

¹ In the collection of the Department of Zoology of the University of California. The other specimens are in the Museum of Vertebrate Zoology of the same institution.

Phrynosoma blainvilliei frontale (Van Denburgh) Bryant
California Horned Lizard

Phrynosoma blainvilliei Gray (1839), p. 96, pl. 29, fig. 1.

Phrynosoma coronata Holbrook (1842), pp. 97-100, pl. 13.

Phrynosoma frontalis Van Denburgh (1894), pp. 296-298.

Phrynosoma frontale Van Denburgh (1897), pp. 93-98.

EXTERNAL CHARACTERISTICS

Diagnostic Characters: Head spines usually smaller and narrower than those of *P. blainvilliei blainvilliei* and very much grooved; small interoccipital spine present; nostrils on the line joining the superciliary ridge with the end of the snout; snout not separated from frontal region by a prominent angle; temporal spines three to six on each side; head plates nearly equal-sized, flat, and covered with numerous ridges and granulations; sublabials, spinose and continued posteriorly by small plates; below the rictus a large, broad infrarictal spine followed by a smaller conical one; enlarged gular scales in three or more double rows with apices pointing outward; peripheral spines in two widely separated rows, the upper being the largest; back and tail covered with large scattered scales, which are strongly keeled and tubercular, set among smaller scales and granules; ventral scales smooth; tail conical and fringed by a row of widely separated trihedral spines; tympanum not covered with scales; femoral pores in long series (12-18).

Description: The two occipital horns and the interoccipital are usually narrower and smaller than those of *P. b. blainvilliei* and the former are very much grooved (pl. 5, fig. 11). The horns of the occipital region are on a higher level than those of the supratemporal region. The nostrils are on the line joining the superciliary ridge with the end of the snout. The snout is separated from the frontal region by a very obtuse angle. Two rows of peripheral spines surround the body, the smaller lower row being separated from the upper by several rows of scales. Three longitudinal rows of enlarged, pointed scales with apices outward, the inner rows being the smallest, are to be found on each side

of the gular region (pl. 5, fig. 11). These rows form an apex at the front of the jaw and continue posteriorly onto the gular folds. The head shields are flat, nearly equal-sized, with numerous ridges and dark-colored granulations (pl. 5, fig. 11). Four or more bony tuberosities are to be found on the parietal region in front of the occipital spines. The temporal horns are four to six in number on each side, the posterior ones being much the largest. The large spinose sublabials number five or six on each side. Below the rictus is a large broad spine followed by a smaller conical one. On each side of the neck are two groups of spines. The lower group is slightly the larger.

The back and tail are covered with large scattered scales which are elevated, keeled, and tubercular, and set among smaller scales and granules. The ventral scales are smooth and equal-sized except on the terminal part of the tail, where they become keeled. A single row of lateral trihedral spines fringes the tail, which possesses a small group of slender spines just behind the thigh. On the anterior portion of the arm and thigh the scales are large, pointed, and keeled. The tympanum is not covered with scales. A long series (12-18) of femoral pores is present. Males have enlarged postanal plates (pl. 5, fig. 12). See table of measurements for dimensions and proportions of the lizard.

The coloration is usually gray or slate to brown, rarely to red. A large brown patch on each side of the neck is darker around the upper edges (pl. 5, fig. 11). Large dark brown cross-bands, posteriorly edged with a light band, usually eight in number, are found on the back and tail. The keels of the enlarged tubercular scales of the back are generally dark brown in color. The head is yellowish white or slaty gray. On the ventral surface the prevailing color is yellow or yellowish white with irregular black blotches (pl. 5, fig. 11). For general color pattern see plate 5, figure 11.

The sole character on which Van Denburgh (1897) based his description of this form as a new species, was upon the appearance of the head plates, those of *blainvilliei* being convex and almost smooth, whereas those of *frontale*, are flat, ridged, and granulated. In addition I have found that several enlarged

scales are present on the central part of the forehead in *blainvillei*, whereas the scales of this region are about equal in size in *frontale*. These characters are all very superficial and can hardly be considered sufficient to separate species. They indicate rather, a differentiation due to geographical location and are therefore better classed as subspecies, under the names *P. blainvillei blainvillei* and *P. blainvillei frontale*. The fact that these two forms intergrade along the line of their contact greatly strengthens this idea.

OSTEOLOGY

But two minor differences from the osteology as described under *Phrynosoma blainvillei blainvillei* were found in this subspecies. In *frontale* the occipital horns are usually narrower and oftentimes more erect. In the skull studied, the pineal foramen, instead of piercing the parietal, is at the coronal suture. Both of these characters vary so widely that they cannot be considered diagnostic. The pineal foramen in *blainvillei* is separated from the coronal suture by only a very narrow strip of bone. As the lizard grows older and the bones become more strongly ossified this differentiation may take place.

HABITS

Several articles on the ability of this horned lizard to "eject blood" have been written. Vernon Bailey, collecting one of these lizards at Kernville, California, had it eject blood from each of its eyes (Stejneger, 1893). Later the same specimen became the subject of an article by O. P. Hay (1892). Dr. Van Denburgh (1897) has recorded the experience of a Mr. Denton with a *P. blainvillei frontale*, and adds that he has twice witnessed the strange performance.

P. b. frontale is the only known horned lizard which inhabits the forest belt. In the vicinity of Pacific Grove, Monterey County, it has been found within the forest shade, closely imitating in color the carpet of pine needles.

DISTRIBUTION

Van Denburgh (1897), in describing this form, suggested an intergradation with *P. b. blainvilliei* in Santa Barbara or Ventura counties. In my material this intergradation would seem to take place in Los Angeles County. A series of specimens from the northern counties of the state shows distinctly *frontale* characteristics until Los Angeles County is reached. Two specimens from the northern part of this county (San Francisquito Cañon, Tuhunga Valley) have equal-sized head scales, very much ridged and granulated, which would show them to be *frontale*. Specimens from eastern Los Angeles County (Claremont) and San Bernardino County are plainly *blainvilliei*, having smooth, convex, head scales, those centrally located being the largest. All available specimens from the vicinity of Pasadena, Los Angeles County, however, appear to be intergrades, for the head scales are convex, those centrally located being the largest, characters of *blainvilliei*, but the scales are ridged and granulated, characters of *frontale*. Sufficient material is not at hand to determine what are the limits of this area of distribution in which these subspecies intergrade or to what degree the intergradation prevails.

This subspecies is found commonly all through the San Joaquin and Sacramento basins and on the western slope of the Sierra Nevada. It doubtless crosses over the divide into the territory occupied by *Phrynosoma platyrhinos* in some of the lower passes in this range. Specimens of both species have been taken on the south fork of the Kern River in Kern County. The most northern record for the California horned lizard is from Placer County. It meets *P. b. blainvilliei* in Los Angeles County. No specimens have been recorded from the coastal region north of San Francisco, but southward from this point the species is abundant. The type specimen was collected at Bear Valley, San Benito County.

The specimens studied were taken at the following localities: Tuhunga Valley, San Francisquito Cañon, in Los Angeles County; Matilija, Mt. Pinos, in Ventura County; Santa Maria,

in Santa Barbara County; Fort Tejon, Bakersfield, Walker Pass, Kernville, Walkers Basin, Weldon, Onyx, Bodfish, south fork Kern River near Chimney Creek, and McKittrick, in Kern County; Earlimart, and Tipton, in Tulare County; Livingston, and Los Banos, in Merced County; Ripon, in Stanislaus County; Lemoore, in Kings County; Pacific Grove, in Monterey County; Bear Valley, in San Benito County; Canada Valley, Gilroy, Coyote Creek, Los Gatos, Morgan Hill, Santa Clara, and Mayfield, in Santa Clara County; Searsville, in San Mateo County; Tracy, and Lathrop, in San Joaquin County; Livermore, in Alameda County; Placerville, in El Dorado County, and Colfax, and Forest Hill, in Placer County.

TABLE OF MEASUREMENTS
Phrynosoma blainvillii frontale

Museum number	Sex	Locality	Phrynosoma blainvillii frontale										Ratios to width of head			
			Total length	Length of tail	Width of head	Snout to ear	Length of occ. horns	Length of fore limb	Length of hind limb	Base of 5th toe	Snout to 4th toe	Tail	Hind limb	Snout to ear	Width of head	
93	♂	Bear Valley, San Benito Co., Calif.	137.0	52.0	26.0	19.5	6.0	41.0	54.0	18.0	38.0	39.4	14.2	19.0	23.0	71.0
..... ¹	♂	Mt. Hamilton, Calif.	121.0	40.0	26.0	17.0	8.0	43.0	52.0	16.0	32.5	43.2	14.1	21.5	30.8	65.5
..... ¹	♂	Mt. Hamilton, Calif.	113.0	39.0	23.5	14.5	7.0	35.0	47.0	14.0	34.0	41.6	12.8	20.8	31.1	61.8
1006	♂	Bakersfield, Kern Co., Calif.	116.0	40.0	26.0	16.1	9.0	38.0	47.0	14.0	34.0	40.5	13.8	22.4	34.6	61.5
1211	♂	Matilija, Ventura Co., Calif.	95.0	29.0	22.0	14.0	6.5	32.0	41.0	12.0	30.0	42.2	14.7	23.1	29.5	63.8
1002	♀	Bakersfield, Kern Co., Calif.	120.0	31.0	27.0	17.0	9.0	37.0	47.0	16.0	26.0	39.2	14.1	22.5	33.2	63.0
..... ¹	♀	Pajaro Road, Calif.	124.0	37.0	27.0	16.5	7.0	42.0	53.0	17.0	29.5	42.7	13.3	21.8	26.0	61.1
875	♀	Mt. Pinos, Ventura Co., Calif.	131.0	40.0	27.5	17.0	9.0	40.0	50.0	15.0	30.5	38.2	13.0	21.0	32.7	62.0
1210	♀	Matilija, Ventura Co., Calif.	114.0	36.0	26.0	17.5	9.0	38.0	48.0	15.0	31.0	42.1	12.5	22.8	34.6	67.3
1212	♀	Matilija, Ventura Co., Calif.	134.0	42.0	28.5	18.0	8.0	43.0	53.0	17.0	31.5	39.6	13.4	21.3	28.0	63.2
Average of males			116.4	40.0	24.7	16.2	7.2	37.8	48.2	14.8	33.7	41.3	13.9	21.3	29.8	64.7
Average of females			124.6	37.2	27.2	17.2	8.4	40.0	50.2	16.0	29.7	40.3	13.2	21.8	30.9	63.3
Average			120.5	38.6	25.9	16.7	7.8	38.9	49.2	15.4	31.7	40.8	13.5	21.5	30.3	64.0

¹ In the collection of the Department of Zoology of the University of California. The other specimens are in the Museum of Vertebrate Zoology of the same institution.

Phrynosoma platyrhinos Girard

Desert Horned Lizard

Doliosaurus platyrhinos Girard (1858), p. 409.

Phrynosoma platyrhinum Cope (1883), pp. 15, 18.

Phrynosoma platyrhinus Boulenger (1885), p. 247.

Anota platyrhina Cope (1898), pp. 443-447, fig. 81.

Anota calidiarum Cope (1896), pp. 833-836.

Phrynosoma calidiarum Ditmars (1907), p. 157.

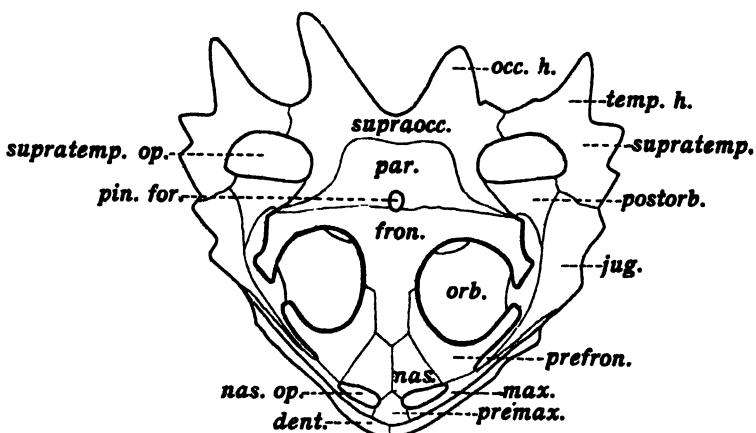


Fig. E. Skull of *Phrynosoma platyrhinos* (Univ. Calif. Mus. Vert. Zool., no. 1301). *dent.*, dentary; *fron.*, frontal; *jug.*, jugal; *max.*, maxillary; *nas.*, nasal; *nas. op.*, nasal opening; *occ. h.*, occipital horn; *orb.*, orbit; *par.*, parietal; *pin. for.*, pineal foramen; *prefron.*, prefrontal; *premax.*, premaxillary; *postorb.*, postorbital; *supraocc.*, supraoccipital; *supratemp.*, supratemporal; *supratemp. op.*, supratemporal opening; *temp. h.*, temporal horn. $\times 2$.

EXTERNAL CHARACTERISTICS

Diagnostic Characters.—Head short and wide; occipital horns of medium size (4-9 mm.), flattened and grooved and but little longer than the temporals; interoccipital represented by an enlarged scale; nostrils above the line joining the superciliary ridge with the end of the snout; temporal horns five to seven on each side, the larger posterior ones pointing in almost the same direction as the occipitals; head plates grooved and ridged and nearly equal sized, except for three enlarged scales in front of the occipital horns; sublabials large and spinose, increasing in size posteriorly; no enlarged infrarictal spine; usually one row of enlarged gular scales on each side, distant from the

median line; peripheral spines in one row, disappearing posteriorly; back and tail with several rows of enlarged, weakly keeled, spinose scales set among finer scales and granules; ventral scales smooth; tail conical and attenuated and fringed with a row of conical scales; tympanum usually entirely covered with scales; femoral pores few (7-8).

Description.—The short wide head is somewhat smaller than is found in the other species (pl. 6, fig. 13). The two occipital horns are of medium size (4-9 mm.), flattened and grooved. An interoccipital is represented by an enlarged scale. The nostrils are situated above the lines joining the supraciliary ridge with the end of the snout. The series of temporal horns numbers five to seven on each side. The posterior two or three are the best developed, the others being mere tubercles. The posterior ones point almost in the same direction as the occipitals. The head shields are small and flat, with the exception of three enlarged scales in front of the occipital horns, and are roughened by granules and ridges. The suprarorbital regions are swollen. The infralabials are nearly equal in size and are acutely angular. Below them and separated from them by a row or two of small scales is a series of large, spinose, sublabial plates which increase in size posteriorly (pl. 6, fig. 14). No enlarged subretial spine is present. But one row of peripheral spines fringes the body. One row of enlarged gular scales, distant from the median line, is present (pl. 6, fig. 14). There are two groups of enlarged scales on each side of the neck, the lower being the larger. The back and tail are covered with several rows of large, weakly keeled, spinose scales, set among finer scales and granules. A rosette of scales surrounds these larger ones. The ventral scales are smooth. The conical tail is attenuated and is fringed by a row of widely separated, conical spines. The limbs are long in comparison with those of other species, and the arm and thigh are fringed anteriorly by a row of enlarged, keeled scales. The tympanum is usually covered with scales, but this character is not constant. A row of widely separated, conspicuous femoral pores, seven to ten on each side, invades the preanal region. Males have enlarged postanal plates (pl. 5, fig. 14). See table of measurements for dimensions and proportions of the lizard.

The general color above is white, gray, or yellow, marbled with brown to black, with oftentimes red markings. The neck patches nearly meet on the median line near the occiput, are short and wide, and often faded in the older specimens. Obscure cross-bands are to be found on the limbs and tail. The head is usually dotted with black, brown, or red. The lower surface is whitish to yellow and usually spotted with black. For general color pattern see plate 5, figure 13.

OSTEOLOGY

Diagnostic Characters.—Horns of occipital region medium sized (5-7 mm.), flattened and grooved; interoccipital horn a small tuberosity; supratemporal horns, three on each element, posterior ones pointing in almost the same direction as the occipitals; jugals with four or five tuberosities; parietal region with three bony tuberosities, in the shape of a triangle, back of the pineal foramen; the edge of the frontal forming the arch over the orbits with elevated plate-like processes; superciliary processes from prefrontals and frontals about equal in length and not meeting; quadrates short and wide (4 x 2 mm.); two to five bony processes on each side of the lower mandible; articulars partly ossified to surangulars; slight evidence of dorsal crest; third sternal ribs attached to xiphoid rods near their base; post-temporal openings small; supratemporal openings about twice as wide as long.

Description.—The alveolar portion of the premaxillary (*premax.*, fig. E) borders the orbit for only a very short distance. The superciliary processes from the prefrontals (*prefron.*) and frontal (*fron.*) are of about equal length and do not meet. A number of raised plate-like processes are to be found on the edge of the frontal bordering the posterior part of the orbit (*orb.*). The occipital horns (*occ. h.*) have their origins close together and are medium in size, flattened, and grooved. The interoccipital horn (*interocc. h.*) is represented by a small tuberosity. The supratemporal horns (*supratemp. h.*) are three in number on each side. The posterior ones are the best developed and point in almost the same direction as the occipitals. Three to five tuberosities are found on each jugal (*jug.*). The vomers

articulate for nearly their whole length, leaving the hiatus to run between them for a proportionally short distance. The basipterygoid processes are long (3-4 mm.). The slender epipterygoids reach the sharp anterior edge of the petrosal. The quadrates are short (4 by 2 mm.).

The lower mandible presents several spinose tuberosities on each side (pl. 2, fig. 5). The coronoids are small and thin. The Meckelian groove is nearly closed with cartilage. The articulars are partly fused to the surangulars, leaving but a faint suture.

A few enlarged neural spines just back of the pectoral girdle show the rudiments of a dorsal crest. The second pair of transverse processes from the sacral vertebrae are small and slender. The well ossified postischial symphysial cartilage is six millimeters in length and is bifid at its tip. The slender transverse processes of the caudal vertebrae are present to near the end of the tail. The transverse processes of the first caudal vertebra are nearly as long as those of the second or third and curve posteriorly, so that their tips almost touch the second pair of processes.

In the skeleton of this species one peculiarity, that of the joining of the third pair of sternal ribs to the xiphoid rods, is interesting (pl. 8, fig. 19). Every other species studied showed the xiphoid rods widely separated from the third pair of sternal ribs. If there were a marked lengthening of the body so that a strengthening of the floating ribs would be of value, this migration of the third pair of ribs could well be understood. The ratio of length to width in *Phrynosoma platyrhinos* is very nearly the same as in the other species, so that this explanation hardly seems sufficient. This character being unique, at least among the five species and subspecies studied, it can well be used as diagnostic of this form. This species and *A. maccalli* alone among the species examined showed a postischial symphysial cartilage with a bifid tip.

HABITS

Phrynosoma platyrhinos is truly a desert species and is found in the most arid and barren places. During the heat of the day it usually keeps in the shade or buries itself beneath the sand,

but in the late afternoon it is seen scurrying across the sand hunting for its insect food.

Specimens of this species show the brightest coloration of any of the horned lizards under discussion. Several specimens from Nevada have bright red markings. As is the case with the other species of the genus, the ground color varies with the surroundings. Mt. Stejneger (1893), in his notes on the reptiles collected on the Death Valley expedition, says: "The specimens collected by the expedition vary from a very pale, in some nearly whitish, drab gray to a vivid brick-red. At Ash Meadows in the Amargosa Desert a very white form was found living on the white alkali soil."

DISTRIBUTION

P. platyrhinos inhabits the Lower Sonoran deserts of the Great Basin from California to Utah. The type locality is Great Salt Lake, Utah. In the mountains it often ranges a short distance into the Upper Sonoran Zone, for it has been taken at an altitude of 5700 feet in the Argus, Funeral, and Panamint mountains. This is the common horned lizard of Nevada and of the Colorado and Mohave deserts of California. No record of its occurrence in northern California is known, but it doubtless does occur in Lassen and Modoc counties, for it is common just across the line in Nevada. In Imperial County, California, this species overlaps the territory occupied by *Anota maccalli*, both species having been taken at Mecca. This locality probably marks its southern limit. Specimens of *P. platyrhinos* and *P. blainvilliei frontale* have been taken in Walker Pass and on the south fork of the Kern River, indicating that an overlapping of distribution areas takes place in this region.

The type locality (Death Valley, California) of a horned lizard described by Cope (1896) under the name *Anota calidiarum* lies within the territory occupied by *P. platyrhinos*. The diagnostic characters used by Cope in his description show *P. calidiarum* (*Anota calidiarum*) to be very closely allied to *P. platyrhinos*. He says: "This species is nearest to the *A. platyrhina* Girard, from which it differs in various respects. The general proportions of all the parts and the coloration are about

as in that species, the difference chiefly appearing in the squamation and the horns. The scales of the head are more subdivided, and the presence of accessory horns is unique in the genus. The simplicity of the lateral fringe is also characteristic, as is also the rudimentary character of the rosette on the neck (Cope, 1898)." Ditmars (1907) describes this species as *Phrynosoma calidiarum*, and says that he has received a specimen from the Gila Desert of Arizona. He calls attention to the erect position of the occipital horns. The photograph which accompanies the description, however, appears to be a *platyrhinos*. Van Denburgh (1897) does not describe this species, but marks it "uncertain."

The type specimen in the U. S. National Museum is the only known example of the species except for the one mentioned by Mr. Ditmars. No material, therefore, is at hand for examination. A study of the figures given by Cope (1898) and his descriptions of the species has convinced me that this is a doubtful form. Dr. Leonard Stejneger, to whom the matter was referred, regards *Phrynosoma calidiarum* as a synonym of *Phrynosoma platyrhinos*.

Specimens of *Phrynosoma platyrhinos* have been recorded from the following localities in California: Coyote Wells, in Imperial County; Mecca, and Palm Springs, in Riverside County; Needles, and Coyote Holes, twenty miles northeast of Daggett, in San Bernardino County; Antelope Valley, in Los Angeles County; Coso Valley, Coso, Ash Creek, ten miles north of Bishop, Independence, head of Borax Flat, and Wild Rose Spring, in Inyo County; and south fork of Kern River near Chimney Creek, Walker Pass, and head of Kelso Valley, in Kern County. In Nevada, specimens have been taken at Vegas Valley, and Indian Spring, in Clark County; Pahrump Valley, Pahranagat Valley, and Panaca, in Lincoln County; Grapevine Mountains, in Esmeralda County; Virginia City, in Storey County; Pyramid Lake, in Washoe County; and head of Humboldt River, Amos, Quinn River Crossing, Pine Forest Mountains, Thousand Creek Ranch, and Leonard Creek, Alder Creek, and Big Creek Ranch, in the Pine Forest Mountains, in Humboldt County.

TABLE OF MEASUREMENTS

Phrynosoma platyrhinos

Number	Sex	Locality	Ratios to total length						Ratios to width of head		
			Total length	Length of tail	Width of head	Snout to eye	Head width	Width of ear	Snout to eye	Head width	Width of eye
<i>Phrynosoma platyrhinos</i>											
1289 ¹	♂	Pine Forest Mts., Humboldt Co., Nev.	120.0	45.0	24.0	6.5	38.0	40.0	10.4	20.0	27.0
1306	♂	Big Creek Ranch, Humboldt Co., Nev.	113.0	42.0	24.0	9.0	36.0	46.0	14.0	37.0	41.3
1283	♂	Quinn River Crossing, Humboldt Co., Nev.	105.0	38.0	21.0	7.0	38.0	47.0	15.0	35.5	44.8
1104	♂	Needles, San Bernardino Co., Calif.	122.0	40.0	22.0	7.5	38.0	50.0	18.0	33.0	41.0
412	♂	Mecca, Riverside Co., Calif.	122.0	46.0	23.0	8.0	39.0	56.0	19.0	38.0	45.9
1290	♀	Pine Forest Mts., Humboldt Co., Nev.	117.0	40.0	22.0	7.0	37.0	49.0	17.0	34.5	42.0
1292	♀	Pine Forest Mts., Humboldt Co., Nev.	112.0	38.0	20.0	4.0	38.0	44.0	14.0	34.0	39.2
1286	♀	Leonard Creek, Humboldt Co., Nev.	108.0	38.0	20.0	6.0	33.0	45.0	16.0	34.5	41.6
1227	♀	Thousands Creek Ranch, Humboldt Co., Nev.	118.0	38.0	21.5	14.0	7.0	40.0	49.0	16.0	32.0
1295 ¹	♀	Big Creek Ranch, Humboldt Co., Nev.	104.0	33.0	20.0	13.5	4.0	36.0	46.0	14.0	32.0
Average of males											
Average of females											
Average											

¹ All of the above specimens are in the Museum of Vertebrate Zoology of the University of California.

Genus **Anota** Hallowell emend.

Dolosaurus Girard (1858), pp. 407-408.

Phrynosoma, Cope (1866), p. 310.

Diagnostic Characters.—Head short and abbreviated; occipital and temporal regions bearing long, smooth spines; cephalic plates small and polygonal; nostrils anterior; sublabial spines large and acute; gular scales small; upper surface of body comparatively smooth, the numerous spinose scales of *Phrynosoma* being greatly reduced in size; body fringed with a triple row of peripheral spines; tail flat; auricular apertures usually concealed by scales; supratemporal openings absent; well-developed transverse processes on the caudal vertebrae.

Description.—Hallowell (1852) recognized in the species *maccalli* a form which differed widely from any horned lizard known at that time, and so placed it in a new genus which he termed *Anota*. He based the division primarily on the character of the auricular aperture, the opening being concealed by scales. This character not being diagnostic, many subsequent writers have classed the type of *Anota* (*Anota maccalli*) in the genus *Phrynosoma* (Cope, 1866; Boulenger, 1885; Van Denburgh, 1897; Ditmars, 1907). Cope (1898), using the single character of the ear opening, included in this genus the species *modestum*, *calidiarum*, *goodeni*, and *platyrhinos*. The present study has shown the character of the ear opening to vary greatly in the species named, some specimens showing the opening entirely closed, whereas others show it to be but partly closed. Even should this character be considered valid, yet the species *maccalli* shows such distinct characters that it should be separated from all other forms of horned lizards found in the United States. The subgeneric name proposed by Girard (1858) includes with *maccalli* the species *platyrhinos* and *modestum*, but his rejection of the name *Anota*, simply because it described a structure as developed in one of the species only, cannot be supported. The grouping together of the desert species as proposed by Girard and Cope would make an admirable division did these species

not show such wide differences in structure. In recognition of the distinct characters of *maccalli* the genus *Anota* is here emended to include this species only, the other species classed by Cope under this genus, being referred to *Phrynosoma* because of their intimate relations to the species of that genus.

The genus *Phrynosoma* is so absolutely distinct from the other iguanids and in turn from all of the *Lacertilia* that any species with the horns, the enlarged tubercular scales of the back, and the peculiarly shaped head characteristic of the horned lizards, is naturally referred to this genus. It is interesting, therefore, that within such a specialized group one species alone should show such divergent specialization as to call for a separate genus. The closure of the supratemporal openings alone seems to justify generic rather than subgeneric separation from the other horned lizards, for this character is without parallel among the *Lacertilia*. Osborn (1903) considered the presence of the supratemporal fenestra so constant that he used it as a character in dividing *Reptilia* into the subclasses, *Synapsida* and *Diapsida*. He says: "The contrast between the elongate cranium and large supratemporal fenestra and the abbreviate cranium and short supratemporal fenestra is one of the striking differences between the *Synapsida* and *Diapsida*." Although he does not discuss the presence of the opening in *Lacertilia*, its presence is inferred to be constant in that the *Lacertilia* are grouped under *Diapsida*.

A thorough examination of all of the horned lizards of the United States showed the presence of the opening. Several of the rarer Mexican species have not been available, but these show close resemblance to other species which possess the supratemporal opening.

An examination of young specimens showed a very small opening, about the size of a pinpoint, to be present, which would lead one to believe that the opening is closed during the period of growth. In adult specimens the opening is entirely roofed over with bone, a suture being left between the parietal and supratemporal elements.

It seems difficult to account for the closure of an opening

that is found in every other species in a class (Diapsida) as far as is known. The intense heat of the desert fails to account for it, for *Phrynosoma platyrhinos*, a co-inhabitant of the same desert, and *P. modestum*, a near neighbor on the east, both show well-developed supratemporal openings. *P. modestum*, although a smaller lizard, presents by far the largest openings. The full development of the horns in *Anota maccalli* might call for a strengthening of the parietal and temporal region. The closure of the opening gives fully four millimeters more of suture in the adult, thus undoubtedly strengthening the horns to a considerable extent. The skull of *A. maccalli* is far more delicate in structure than that in any of the other species. *Phrynosoma blainvilliei blainvilliei* develops horns just as long as those of *maccalli*, but their ratio to the width of the head is much less (see tables of measurements). Then, too, *blainvilliei* has very heavy parietal bones, so that the need of strengthening the horns by means of a longer suture is not so apparent. It seems reasonable to believe, therefore, that in the evolution of this peculiar form there has taken place a strengthening of the horns through a closure of the supratemporal openings by the fusion of the surrounding bony elements.

Several other osteological characters, such as the well-developed spines of the lower mandible and the dome-shaped parietal region, separate the type *maccalli* from other species of horned lizards, but are best not definitely regarded as purely generic characters.

One of the most distinctive external characteristics is the flat tail. No other known species of horned lizards shows this peculiarity. As this flattening of the tail is accompanied by an associated osteological character, well-developed transverse processes on each of the caudal vertebrae, this character can well be considered diagnostic of this genus. Flat-tailed horned lizards as distinguished from other horned lizards would make a well defined group.

Anota maccalli* Hallowell*Flat-tailed Horned Lizard***Anota M'Callii* Hallowell (1852), p. 182.*Doliosaurus mc'calli* Girard (1858), pp. 408-409.*Phrynosoma maccallii* Cope (1866), p. 310.*Phrynosoma m'calli* Van Denburgh (1897), pp. 100-101.

Diagnostic Characters.—Head small; occipital horns long, smooth, and conical; interoccipital horn lacking; nostrils above the line joining the superciliary ridges with the end of the snout;

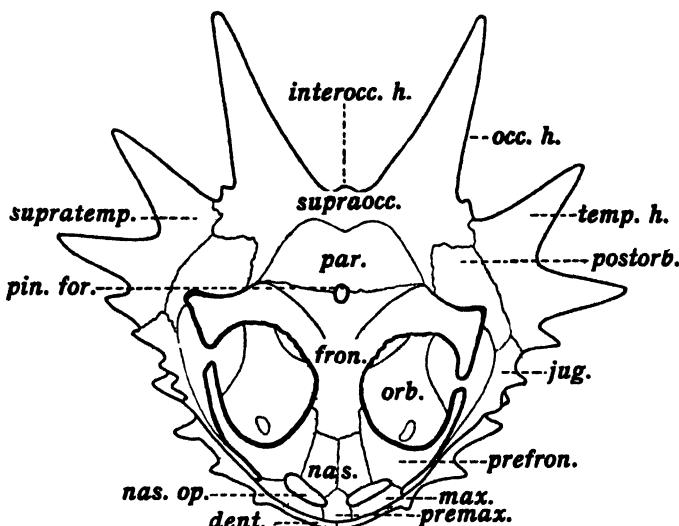


Fig. F. Skull of *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1006). *dent.*, dentary; *fron.*, frontal; *jug.*, jugal; *interocc. h.*, interoccipital horn; *max.* maxillary; *nas.*, nasal; *nas. op.*, nasal opening; *occ. h.*, occipital horn; *orb.*, orbit; *par.*, parietal; *pin. for.*, pineal foramen; *prefron.*, prefrontal; *premax.*, premaxillary; *postorb.*, postorbital; *supraocc.*, supraoccipital; *supratemp.*, supratemporal; *supratemp. op.*, supratemporal opening; *temp. h.*, temporal horn. $\times 2$.

temporal horns five or six on each side, the two posterior sharp and of about equal length; head plates irregular in size and shape; two enlarged plates just back of the pineal eye and one between the occipitals; sublabials large and acute, the middle ones the broadest and longest; no enlarged infrarictal spine; one row of slightly enlarged gulars on each side; the small peripheral spines in three closely set rows, the middle row being the largest;

back and tail with several rows of large, weakly keeled, spinose scales set among fine granule-like scales; ventral scales smooth; tail flat, acute and bordered by a single row of conical spines, every second spine being of smaller size; tympanum entirely concealed with scales; femoral pores in long rows (17-20 on each side) invading the preanal region.

Description.—The head is somewhat smaller than is found in other species (pl. 7, fig. 15). The snout is separated from the frontal region by a very prominent angle. The two occipital horns are long, smooth and conical, and are set close together. The nostrils are above the line joining the superciliary ridge with the end of the snout. There are five or six temporal horns on each side. The two posterior on each side are sharp and of about equal length. The head plates are polygonal, irregular in size and shape, with two enlarged plates just back of the pineal eye and one large one between the occipital horns. A group of enlarged scales is found on the front of the head at the angle with the snout. The supraorbital regions are swollen. The supralabials are somewhat spinose, giving a serrate appearance. The infralabials are small and flat; the sublabials large and acutely spinose (pl. 7, fig. 16). Those in the middle of the rows are usually the broadest and longest. No enlarged subrictal spine is present. One row of slightly enlarged gular scales, not reaching to the apex of the jaw, is found on each side of the gular region (pl. 7, fig. 16). Two small groups of conical spines are situated on each side of the neck. The back and tail present a much smoother appearance than that found in the other species. Several rows of large, weakly keeled, spinose scales are set among small granule-like scales. The enlarged scales are surrounded by a rosette of smaller ones (pl. 7, fig. 15). The ventral scales are smooth. The tail is very flat and tapers gradually to the tip. It is fringed by a row of conical spines, every second one of which is smaller than the preceding one. A short row is also formed on the tail just behind the thigh. The arm and thigh are bordered anteriorly with a row of enlarged keeled scales. The tympanum is entirely covered with scales. The femoral pores are numerous (17-20) and the rows nearly meet medially (pl. 7, fig. 16). Males have enlarged

postanal plates. See table of measurements for dimensions and proportions of the lizard.

The ground color is usually ashy gray or yellowish. Two rows of round, dark brown spots containing a paler center, centered with a brown dot, are arranged on either side of the median line (pl. 7, fig. 15). The neck patches are pale and inconspicuous. A narrow brownish median line leads from the occiput to the tail. Ventrally the color is silvery or yellowish white (pl. 7, fig. 16). The head is unspotted and the horns but little darker in color. Although this description of the coloration will fit many specimens, yet it is by no means the only type, for there are great variations in color. For general color pattern see plate 7, figure 15.

OSTEOLOGY

Diagnostic Characters.—Horns of occipital region long, smooth, and conical; interoccipital horn lacking; supratemporal horns three in number on each element, the posterior two sharp and of about equal length; jugal with three tuberosities on a line above the row of supratemporals; superciliary processes from premaxillaries twice as long as those from frontal; parietal region dome-shaped; postorbitals meeting parietal and supratemporals, thus closing the supratemporal opening; quadrates short (4 mm. in length) and narrow; lower mandible with six spinose tuberosities on each side, the two anterior ones on each side rudimentary; epipterygoids articulating in a depression of the petrosal; articulars not ossified to surangulars; all the caudal vertebrae with well-developed transverse processes.

Description.—The alveolar portion of the premaxillary (*premax.*, fig. F) element is very little wider than the element itself and does not appreciably border the nasal opening (*nas. op.*). The supramaxillary processes are wide and heavy, and articulate with processes from the palatines. The frontal (*fron.*) shows elevations for the enlarged scales bordering the orbit (*orb.*). The prefrontal (*prefron.*) superciliary processes are long (3.5 mm.), arching the orbits for two-thirds of the distance. The frontal superciliary processes are short (1-2 mm.). Small postorbital spines are situated at the lateral angles of the frontal. The parietal (*par.*) region is dome-shaped; the pineal foramen

(*pin. for.*) is at the coronal suture. The two occipital horns (*occ. h.*) are long, smooth, and conical with a small tuberosity at the base of each. They are closely set together, an interoccipital being absent. The postorbitals (*postorb.*) meet the parietal, entirely closing the supratemporal opening. On each of the supratemporal (*supratemp.*) elements are two sharp, recurved horns with a third smaller anterior one. The marked upward curvature of the temporal horns is a characteristic of this species only. The posterior temporal horns are sharp and about equal in length. Each jugal (*jug.*) presents three tuberosities. The occipital condyle is trilobate in shape. The quadrates are small and narrow. The vomers slant back and up and are separated for over half their length by a wide hiatus. The processes from the basipterygoids are slender. The short epipterygoids fit into depressions on the petrossal.

Meckel's groove is long and narrow. Each angular presents three, almost equal sized, conical spines and each dentary (*dent.*) three, the two anterior of which are rudimentary. The articulars project downward and are not ossified to the surangulars.

The supporting of the spiny scales on the mandibles by bony tuberosities is peculiar to this species and to *Phrynosoma platyrhinos*. In this character we find a fine example of a purely dermal structure becoming more deep-seated and a bony support being developed. In *P. d. douglassi* and *P. b. blainvilliei* no spinose ossifications are to be found on the lower mandible. However, well-developed spinose scales are present. In *P. platyrhinos* and *A. maccalli* the scales present the same appearance exteriorly, but are supported by a bony spine. The same can be noted on the jugal and supraorbital regions (pl. 2). There is, therefore, a growing tendency in some species to support the dermal scales by bony spines. That the occipital spines were developed by the same stages seems probable. The bony spines appear to be simply processes from the bone itself and not small ossifications inside the scale which secondarily fuse with the bone.

The orbital opening (*orb.*) is oval in shape. The supratemporal openings are completely roofed with bone by the meeting of the parietal (*par.*), supratemporal (*supratemp.*), and post-

orbital (*postorb.*) elements. The posttemporal openings are small. The nasal openings (pl. 2, fig. 6) are anterior.

All of the neural spines are small and about equal in size. The partially ossified postischial symphysial cartilage is bifid at its tip and very nearly reaches to the caudal vertebrae (fig. B). Each caudal vertebra is supplied with well-developed transverse processes. The first pair of processes are short and curve posteriorly. The second and third pair are longest.

Comparison.—Yarrow and Henshaw (1878) record several specimens of this species from the Mohave Desert. Cope (1898), however, places specimens in the U. S. National Museum, bearing the same number and locality, under *platyrhinos*, and notes but three specimens of *maccalli*, all of which are from eastern San Diego County (Imperial County). Thus it appears that *P. platyrhinos* was mistaken by some former authors for the rarer species, *A. maccalli*. The two lizards are very different, as can be seen by the following table of the more striking differences (pl. 6, pl. 7; pl. 2, figs. 5, 6; figs. E, F).

COMPARISON OF *Phrynosoma platyrhinos* AND *Anota maccalli*

<i>Phrynosoma platyrhinos</i>	<i>Anota maccalli</i>
1. Horns grooved and short.	Horns smooth and long.
2. Two or three well-developed temporal horns.	Five or six well-developed temporal horns.
3. One row of peripheral spines.	Three closely-set rows of peripheral spines.
4. Tail rounded.	Tail flat.
5. Femoral pores 7-12 on each side.	Femoral pores 17-20 on each side.
6. No dark median dorsal line.	Dark median dorsal line.
7. Supratemporal openings present.	Supratemporal openings absent.
8. Third sternal ribs attached to xiphoid rods.	Third sternal ribs attached to sternum.

HABITS

Whether this species has any characteristic habits is not known. The stomach of a specimen was found to contain red ants and quite a little sand, which had probably been picked up with the insects. The coloration is of a light shade, closely imitating the light coloration of the desert sand and alkali soil.

DISTRIBUTION

The type locality of *Anota maccalli* is the Great Desert of the Colorado between Vallecito and Camp Yuma about 160 miles east of San Diego. All of the specimens in the Museum of Vertebrate Zoology are from the same general locality. One specimen in the collection of the Department of Zoology from Sonora, Mexico, indicates its occurrence over the border in Mexico. A list of the specimens studied follows:

LIST OF SPECIMENS OF *Anota maccalli*

Museum number	Sex	Locality	Date	Collector
1001	♀	Coyote Well, Imperial County, California	March 30, 1909	F. Stephens
1007	♀	Salton Lake, Imperial County, California	April 24, 1909	F. Stevens
1019	♀	Salton Lake, Imperial County, California	April 27, 1909	F. Stephens
449	♀	Mecca, Riverside County, California	March 31, 1908	C. H. Richardson, Jr.
450	♀	Mecca, Riverside County, California	March 25, 1908	C. H. Richardson, Jr.
447	♂	Mecca, Riverside County, California	March 31, 1908	W. P. Taylor
448	♂	Mecca, Riverside County, California	March 31, 1908	W. P. Taylor
Dept. Zool.	♀?	Sonora, Mexico		C. E. Hays

TABLE OF MEASUREMENTS

Collection number	Sex	Locality	<i>Anota macalli</i>	Ratios to total length		Ratios to width of head	
				Width of head	Length of tail	Width of ear	Length of hind limb
1007	♀	Salton Lake, Imperial Co., Calif.	128.0	47.0	30.5	14.0	12.0
1001	♀	Coyote Well, Imperial Co., Calif.	100.0	36.0	24.0	12.0	10.0
1019	♀	Salton Lake, Imperial Co., Calif.	84.0	30.0	21.0	10.0	8.0
449	♀	Mecca, Riverside Co., Calif.	69.0	20.5	19.0	8.5	7.0
450	♀	Mecca, Riverside Co., Calif.	95.0	34.5	22.0	11.0	8.5
447	♂	Mecca, Riverside Co., Calif.	78.0	25.5	21.0	9.0	7.5
448	♂	Mecca, Riverside Co., Calif.	85.0	29.0	23.0	11.0	10.5
..... ¹	♀?	Sonora, Mexico	91.0	32.5	21.0	10.0	8.0
Average of males			81.5	27.2	22.0	10.0	9.0
Average of females			94.5	33.4	22.9	10.9	8.9
Average			88.0	30.3	22.4	10.4	8.9

¹ In the collection of the Department of Zoology of the University of California. The others are in the collection of the Museum of Vertebrate Zoology of the same institution.

SUMMARY

1. The bases for generic and specific distinction among the horned lizards have not as yet been generally accepted owing to the difficulty experienced in finding dependable characters. This study of the horned lizards of California and Nevada shows that there are diagnostic osteological characters which in addition to the characters now separating the species might, by the working out of a key from a complete set of specimens of all the species, furnish the necessary characters for a revision of the genus.

2. A study of the osteology of the different species inhabiting California and Nevada was productive of at least four interesting features. (a) The closure of the supratemporal openings by the meeting of the postorbital, supratemporal, and parietal elements in *Anota maccalli*, a character heretofore unknown among the Lacertilia. (b) The attachment of the third sternal ribs to the xiphoid rods, a peculiarity of *Phrynosoma platyrhinos*. (c) A supporting of epidermal sublabial spines by bony processes from the lower mandibles in *Phrynosoma platyrhinos* and *Anota maccalli*. (d) The presence in all of the species of a well-developed postischial symphysial cartilage which, in some species, showed a tendency to ossify.

3. A contribution to the slight knowledge of the "ejection of blood" by horned lizards was afforded by certain experiments carried on by the writer. A few notes on the hibernation of a horned lizard adds something to the limited knowledge of this habit.

4. Five species and subspecies of horned lizards inhabit the states of California and Nevada, each species and subspecies occupying an area fairly well defined. An overlapping of these areas of distribution takes place in at least three localities.

5. The species known as *Phrynosoma blainvilliei* and *Phrynosoma frontale* are separated by very subordinate characters (characters much less diagnostic than those separating other species of horned lizards) and show an intergradation at the line of contact of their areas of distribution. They are therefore but geographical races and are reduced to subspecific rank

under the names *Phrynosoma blainvilliei blainvilliei* and *Phrynosoma blainvilliei frontale*.

6. The horned lizard, *Anota maccalli* (*Phrynosoma maccalli*), is distinct from all other horned lizards. The closure of the supratemporal openings is unknown in any other lacertilian. In recognition of this and its many other differences the genus in which it was originally described has been emended to include this species only.

7. A comparison of the tables of measurements shows that the subspecies differ very little in size, whereas the species differ widely in this respect.

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PLATE 1

Fig. 1. Side view of a living specimen of Blainville's horned lizard, *Phrynosoma blainvilliei blainvilliei*. Note the horns of the occipital and temporal regions; the postorbital spines; the sublabial spines; the gular folds; the large, keeled, tubercular spines of the back; the small granular scales of the back; the smooth, equal-sized scales of the ventral surface; the two widely separated rows of peripheral spines; the row of enlarged scales on the anterior surfaces of arm and thigh; and the neck patch. Approximately life size.

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[BRYANT] PLATE I



PLATE 2

Fig. 2. Skull of *Phrynosoma douglassi douglassi* (Zool. Dept.). Note the rudimentary occipital horns; the lack of spines on the jugal elements; the large supratemporal openings; and the position of the nasal openings. $\times 1\frac{1}{2}$.

Fig. 3. Skull of *Phrynosoma blainvilliei frontale* (Zool. Dept.). Note the well-developed occipital and temporal horns; the interoccipital horn; the spines on the jugal elements; the supratemporal openings; the position of the pineal foramen; and the position of the nasal openings. $\times 1\frac{1}{2}$.

Fig. 4. Skull of *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 272). Note the well-developed occipital and temporal horns; the interoccipital horn; the spines on the jugal elements; the supratemporal openings; the position of the pineal foramen; and the position of the nasal openings. $\times 1\frac{1}{2}$.

Fig. 5. Skull of *Phrynosoma platyrhinos* (Univ. Calif. Mus. Vert. Zool., no. 1301). Note the short occipital and temporal horns; the spines of the jugal elements; the rudimentary spines of the maxillaries; the supratemporal openings; and the position of the nasal openings. $\times 1\frac{1}{2}$.

Fig. 6. Skull of *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1006). Note the long, conical occipital horns; the well developed second temporal horns; the spines of the jugal elements; the well developed spines of the maxillaries; the closure of the supratemporal openings; the dome-shaped parietal region; and the position of the nasal openings. $\times 1\frac{1}{2}$.

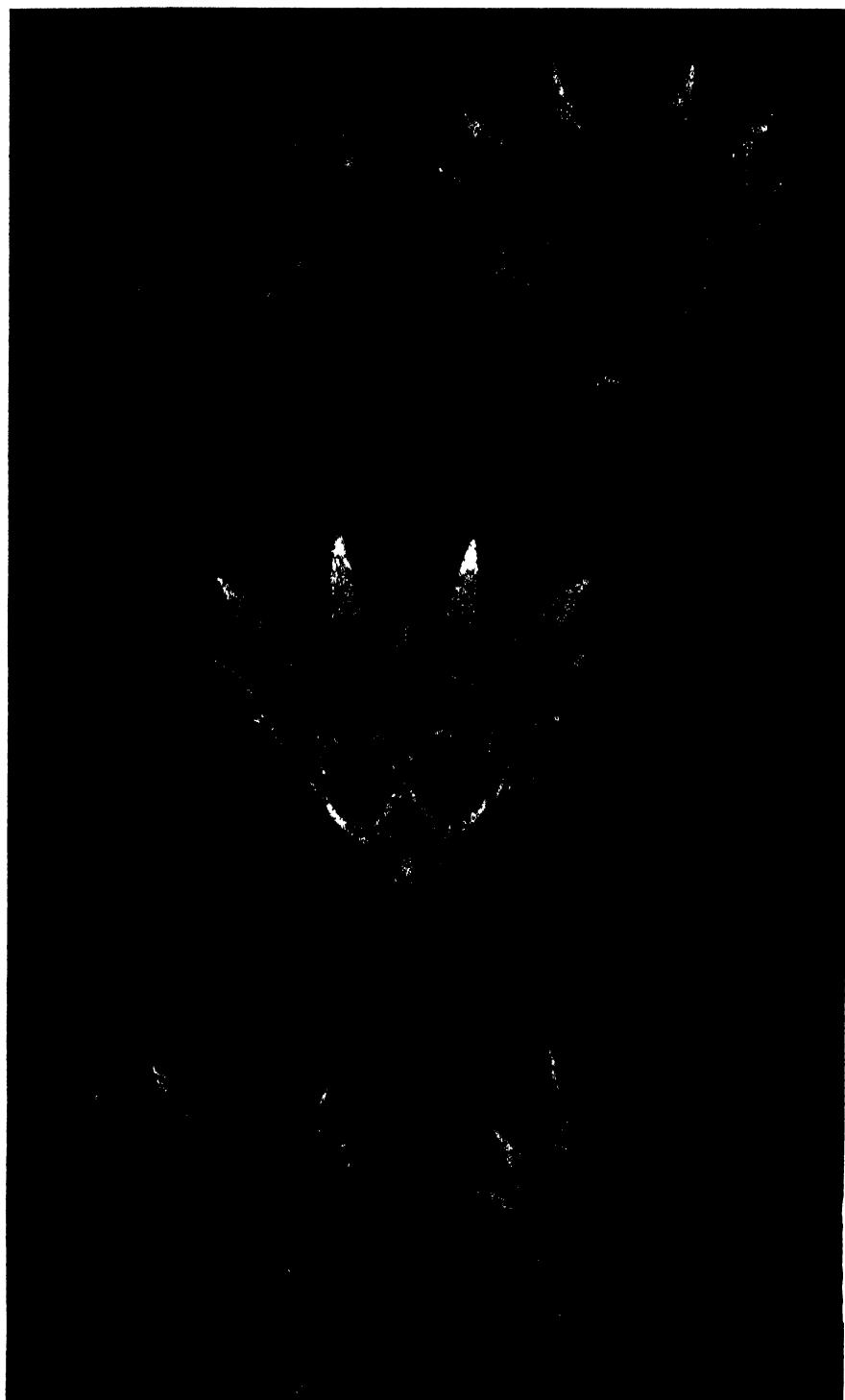


PLATE 3

Fig. 7. Dorsal view of ♀ *Phrynosoma douglassi douglassi* (Dept. Zool.). Note the small size; the rudimentary occipital horns; the temporal horns which project farther posteriorly than the occipitals; the scalation of the head; the attenuated tail; the single row of peripheral spines; and the color pattern. Approximately life size.

Fig. 8. Ventral view of ♀ *Phrynosoma douglassi douglassi* (Dept. Zool.). Note the small sublabials; the equal-sized gular scales; and the long series of femoral pores. Approximately life size.

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[BRYANT] PLATE 3

PLATE 4

Fig. 9. Dorsal view of ♀ *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 60). Note the flattened, grooved occipital horns; the temporal horns; the smooth, convex head shields, those in the center being the largest; the double row of peripheral spines; and the color pattern. Approximately life size.

Fig. 10. Ventral view of ♀ *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 60). Note the large sublabial plates; the three rows of enlarged gular scales; the widely separated rows of peripheral spines; and the femoral pores. Approximately life size.

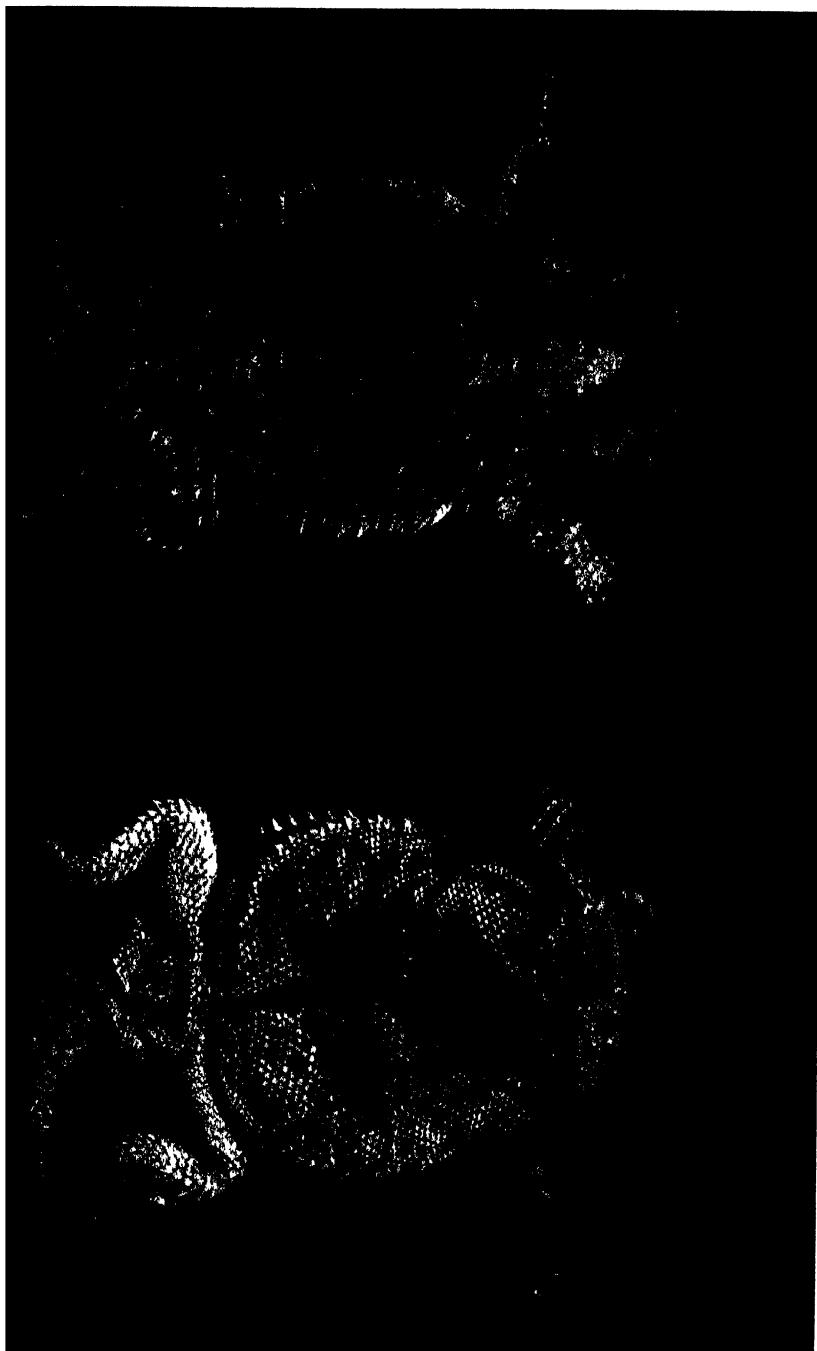


PLATE 5

Fig. 11. Dorsal view of ♂ *Phrynosoma blainvilliei frontale* (Dept. Zool.). Note the narrow occipital horns; the temporal horns; the ridged and granulated, equal-sized head shields; the double row of peripheral spines; and the color pattern. Approximately life size.

Fig. 12. Ventral view of ♂ *Phrynosoma blainvilliei frontale* (Dept. Zool.). Note the large sublabial plates; the three rows of enlarged gular scales; the femoral pores; and the enlarged postanal plates. Approximately life size.

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[BRYANT] PLATE 5

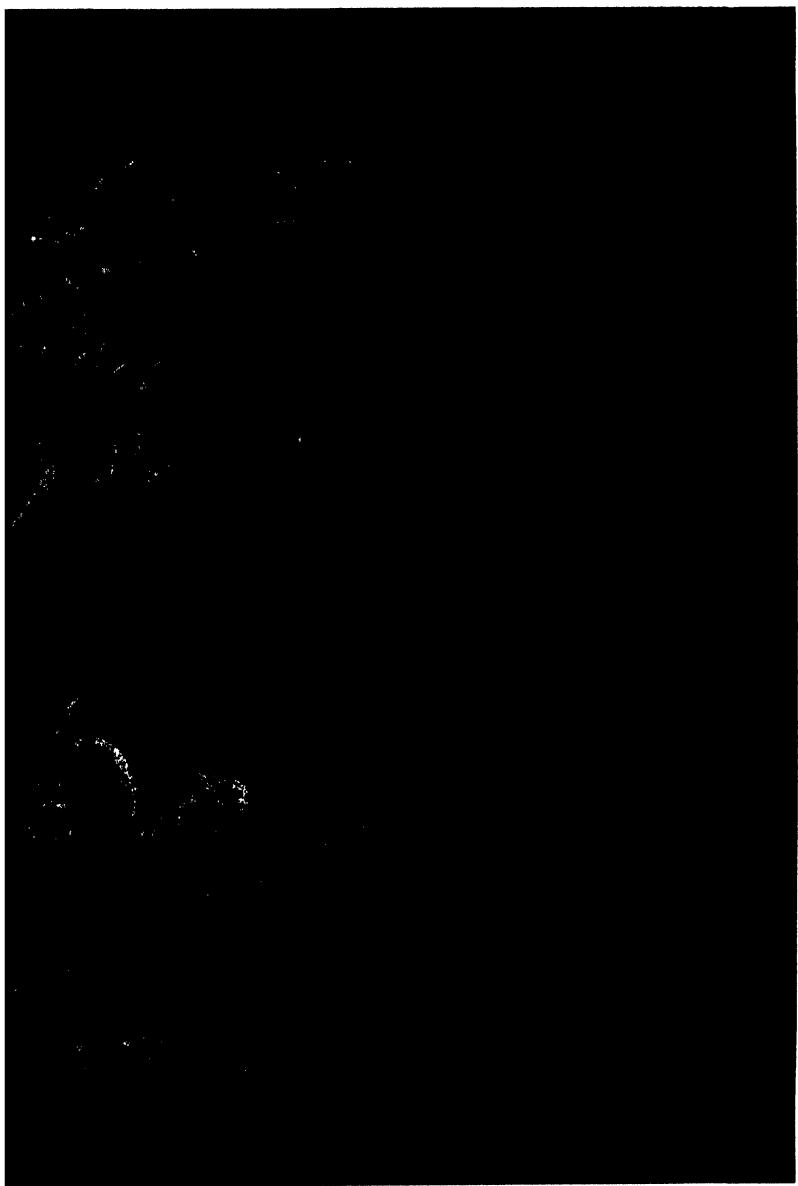


PLATE 6

Fig. 13. Dorsal view of ♂ *Phrynosoma platyrhinos* (Univ. Calif. Mus. Vert. Zool., no. 1311). Note the short occipital horns; the temporal horns; the small equal-sized head shields; the single row of peripheral spines; and the color pattern. Approximately life size.

Fig. 14. Ventral view of ♂ *Phrynosoma platyrhinos* (Univ. Calif. Mus. Vert. Zool., no. 1311). Note the large sublabial plates; the equal-sized gular scales; the single row of peripheral spines; the femoral pores and the enlarged postanal plates. Approximately life size.

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[BRYANT] PLATE 6

PLATE 7

Fig. 15. Dorsal view of ♀ *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1007). Note the long, smooth occipital horns; the recurved temporal horns; the enlarged head shields of the parietal region; the reduced scales of the back; the flattened tail; the triple row of peripheral spines; and the color pattern. Approximately life size.

Fig. 16. Ventral view of ♀ *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1007). Note the large, spinose sublabials; the single row of enlarged gular scales; the triple row of peripheral spines; the flattened tail; and the long series of femoral pores. Approximately life size.

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[BRYANT] PLATE 7

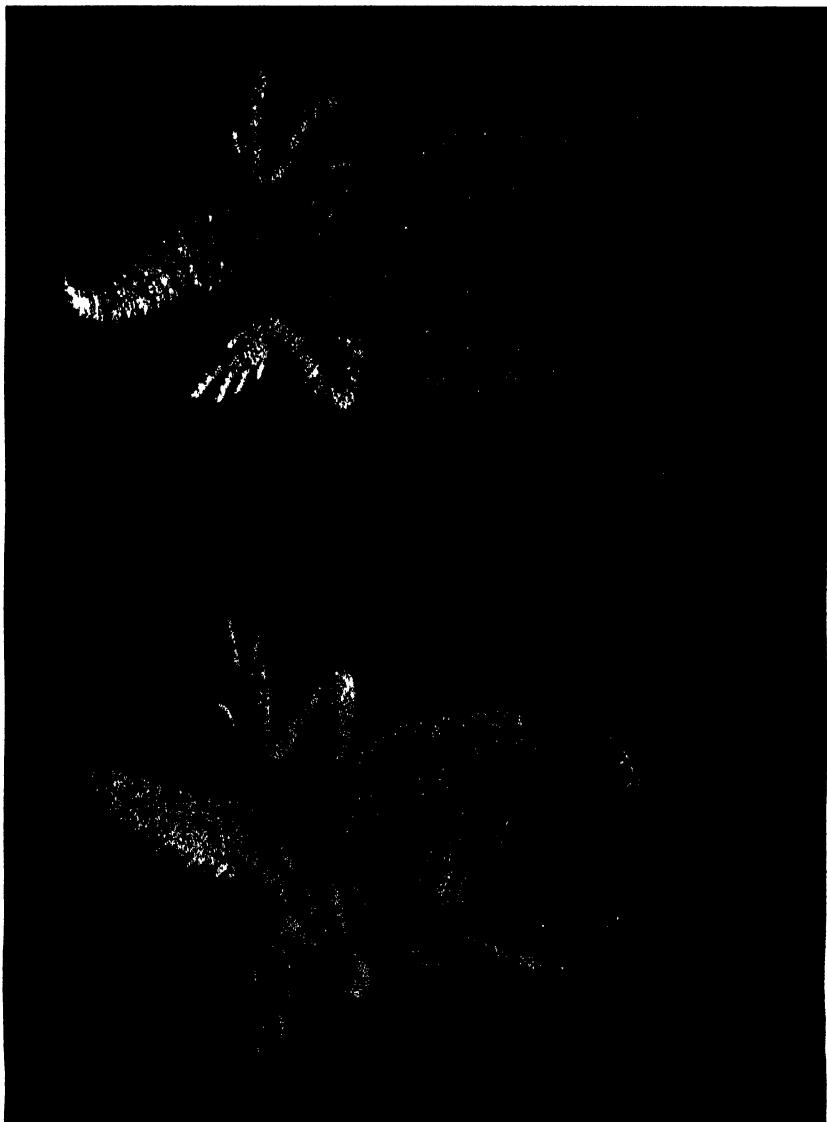


Fig. 17. Sternum of *Phrynosoma douglassi douglassi* (Dept. Zool.). $\times 1\frac{1}{2}$.

Fig. 18. Sternum of *Phrynosoma blainvilliei blainvilliei* (Univ. Calif. Mus. Vert. Zool., no. 272). $\times 1\frac{1}{2}$.

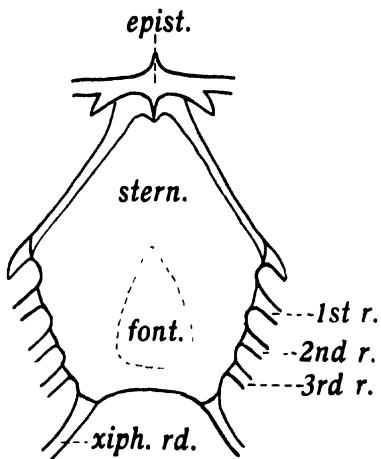
Fig. 19. Sternum of *Phrynosoma platyrhinos* (Univ. Calif. Mus. Vert. Zool., no. 1301). $\times 1\frac{1}{2}$.

Fig. 20. Sternum of *Anota maccalli* (Univ. Calif. Mus. Vert. Zool., no. 1006). $\times 1\frac{1}{2}$.

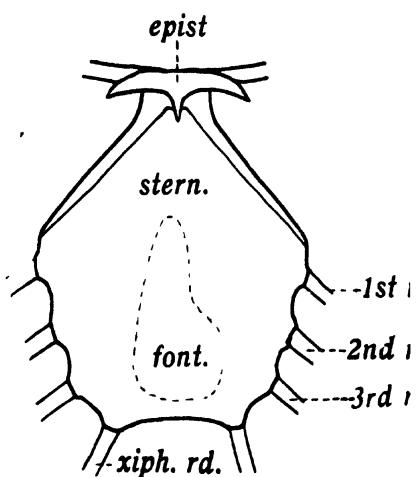
ABBREVIATIONS

1st r., first rib.
2nd r., second rib.
3rd r., third rib.
epist., episternum.

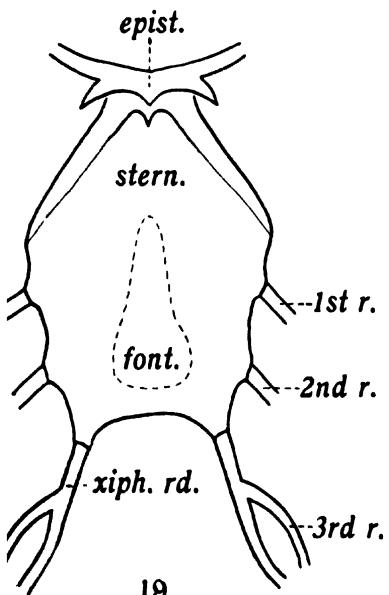
font., fontanelle.
stern., sternum.
xiph. rd., xiphoid rod.



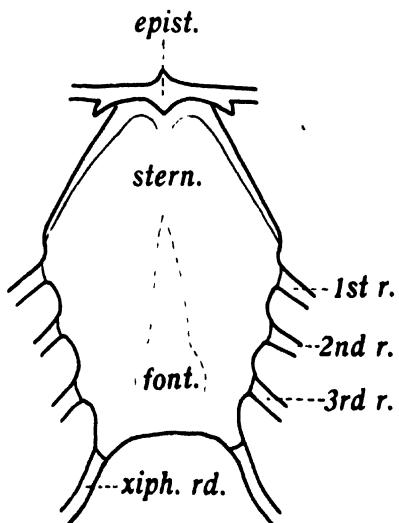
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ON A LYMPHOID STRUCTURE LYING
OVER THE MYELENCEPHALON
OF *LEPISOSTEUS*

BY

ASA C. CHANDLER

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INTRODUCTION

The present paper is a preliminary report on a peculiar gland-like, lymphoid structure discovered over the myelencephalon of *Lepisosteus* while dissecting out the brain in the laboratory of Professor B. G. Wilder, at Cornell University, during the fall of 1910. The work was begun in Cornell University during the college year 1910-11, and later carried on in the Zoological Laboratory at the University of California.

Grateful acknowledgments are here made to Professors C. A. Kofoed and J. Frank Daniel, of the University of California,

and to Professors H. D. Reed, B. F. Kingsbury and W. A. Hilton, of Cornell University, for their supervision and assistance, as well as for the material used, and to Professor B. G. Wilder for his helpful advice and the free use which he allowed of the specimens in his neurological collection.

The structure here described, which I shall provisionally call the myelencephalic gland, was discovered while dissecting out the brain of a long-nosed gar, *Lepisosteus osseus*. While dissecting away the cartilage bit by bit in the region of the hind brain, there was noted a deeply pigmented mass of tissue lying over the myelencephalon, and directly behind the cerebellum. The first inclination was to tear this off with the cartilage and dura mater as merely a pigmented mass of connective tissue, such as often fills the subdural space in teleosts (see Wiedersheim, 1909, fig. 200, p. 294). Since, however, it was seen to have a rather definite form, and to be in closer relation to the brain than to any other part of the head, it was left in position, and carefully dissected out with the brain, to the pial covering of which it was firmly attached.

Though many eminent and competent scientists have worked over the brain of *Lepisosteus*, the myelencephalic gland seems almost universally to have been overlooked. The only reference to it which could be found in the literature on the brain of the ganoids is by Herrick (1891). In his plate 13, figure 9, he figures the dorsal aspect of the brain of *Lepisosteus osseus*, showing the structure in question lying over the myelencephalon. No reference is made to it in the text, and in the description of the figure he merely says: "The bilobed mass lying behind the cerebellum is not of a nervous character." But, as pointed out by Wilder (1891), the membranous parieties of the brain are an important morphological feature of the organ, and should be considered in any treatment of the brain as a whole. As will be shown later, the "bilobed mass" of Herrick is in direct connection with the parieties of the brain, and therefore should not be omitted from a morphological study of the brain because it is not of nervous tissue.

Parker and Balfour (1882) carefully worked out the brain of the adult *Lepisosteus*, and demonstrated the delicate thin-

walled "vesicle of the thalamencephalon," which had previously escaped notice and is readily destroyed in dissection, yet they make no reference to any gland-like structure lying over the myelencephalon, and the usual opening into the fourth ventricle is shown in their figure. They also made sections of the entire head of embryos up to the 26 mm. stage in working out the development of the brain, but, since the gland is not recognizable, as such, up to that stage, it escaped their notice again.

In tearing off the gland in a dissection of the brain, it is impossible not to tear off the posterior medullary velum with it, which accounts for the foramen of Magendie usually shown in figures of the brain of *Lepisosteus*, as seen in the figures of Busch (1848), Mayer (1864), Owen (1868, vol. 1, fig. 174), Huxley (1872, fig. 38), Wilder (1875, pl. 2, fig. 7), Parker and Balfour (1882, pl. 25, fig. 47B), and Allen (1907, pl. 6, figs. 11 and 12). Kingsbury (1897, pl. 6, fig. 5) has a diagrammatic sketch of a cross-section of the myelencephalon in which he shows the roof of the fourth ventricle undisturbed, but without the gland.

OCCURRENCE AND HOMOLOGY

The possibility that this gland might be an abnormal development presented itself, and to determine this point two other specimens of *Lepisosteus osseus* were dissected. The same structure was found in each of them, and was of the same size and shape. It was also found in *Lepisosteus platostomus*, only one specimen of which was available. No example of *L. tristaechus*, or alligator gar, could be obtained for dissection, but on account of the similarity of this species to *L. platostomus* in other respects, and also because of the very close similarity of the gland in the two more divergent species examined, it is probable that this organ will be found in the third species.

It was thought that some such development would be found in other types of ganoid fishes, and in the hope of finding something at least suggestive of it, numerous specimens of ganoid brains in the collection of Dr. Wilder were examined, including examples of *Acipenser*, *Scaphirhynchus*, *Polyodon*, and *Amia*. In none of these, however, could any indication of it be found,

though the possibility exists that in some it may have been present, and have been torn off in dissection. *Polyodon* has a very deeply pigmented pial covering of the brain, but it remains thin and membranous over the fourth ventricle. I myself exposed several brains of *Amia* with the myelencephalic gland especially in mind and found no trace of such a gland there. This was unexpected, since *Amia* is without doubt the form nearest allied to *Lepisosteus*.

In an article on the central nervous system of *Proptopterus annectens*, only the preliminary report of which was accessible to me, Burckhardt (1892) figures the dorsum of this dipnoan brain with a structure possessing numerous diverticula lying over the hind-brain, which he calls the "saccus endolymphaticus." This figure is reproduced by Wiedersheim (1909, fig. 201A, p. 296). In a longitudinal section of the same brain (fig. 202B in Wiedersheim) this "saccus" has seemingly been removed, as the myelencephalon is covered only by the much folded choroid plexus. Whether or not Burckhardt's "saccus endolymphaticus" of *Proptopterus* is in any way related to the myelencephalic gland in *Lepisosteus*, I am unable to say at the present time, but judging from the name and its appearance in the figure, it is highly improbable. If this should be found to be homologous, it is all the more strange that it does not appear in *Amia*.

GENERAL MORPHOLOGY

The general form of the gland in *Lepisosteus osseus* is not bilobed as described by Herrick (1891), but it is trilobed. The main body of the gland is slightly wider than long, and is thickened just cephalad of the middle, sloping off towards the front and back, and with a pronounced median sulcus caudally, causing the posterior border to be emarginate. From the antero-lateral angles there projects on either side an ear-like lobe, very definite and constant in shape and size, connected with the main body by a rather slender neck (fig. A). These ear-like projections are entirely surrounded by cartilage, making their dissection rather difficult, although they readily hold their shape and position when freed from the cartilage.

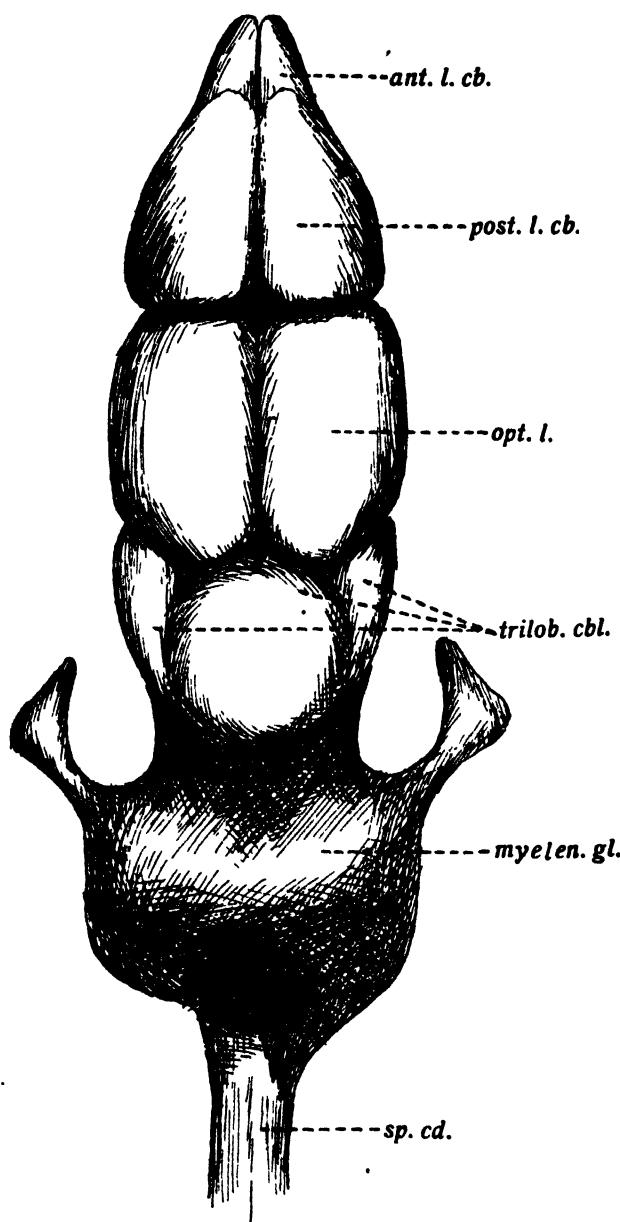


Fig. A. Dorsal aspect of brain of *Lepisosteus osseus*, with myelencephalic gland in situ. $\times 10$. *ant. l. cb.*, anterior lobe of cerebrum; *post. l. cb.*, posterior lobe of cerebrum; *opt. l.*, optic lobe; *trilob. cb.*, trilobed cerebellum; *myelen. gl.*, myelencephalic gland; *sp. cd.*, spinal cord.

In *Lepisosteus platostomus* the gland is almost identical in form to that in *L. osseus*, but the ear-like projections are relatively shorter and stouter than in any specimen of the latter species which I have examined.

The size of the gland as compared with the rest of the brain is considerable. The width of the main body in a 25 cm. specimen is slightly greater than the width of the optic lobes, which form the widest dimensions of the brain, while the width from tip to tip of the lateral lobes is more than twice that of the cerebrum at its greatest width. Its length is approximately that of the cerebellum, and its thickness such that it attains the level of the dorsum of the cerebellum. In adults the size of the gland as compared with the rest of the brain is even greater than this.

The entire brain of *Lepisosteus* is covered by a deeply pigmented membrane which has a peculiar metallic appearance, in which the enormous pigment cells appear under the binocular microscope as a sprinkling of pepper. This covering membrane seems to be directly continuous with the covering of the myelencephalic gland, or with the gland itself, since in microscopic section there is no distinctly differentiated outer covering. In other words, the structure seems to be a very highly developed and enlarged portion of the pigmented covering of the brain.

HISTOLOGY

In order to determine the histological structure of the myelencephalic gland, the best specimen available was fixed in formalin, imbedded in paraffin, and cut in sections 12 microns in thickness. The sections were then stained in Delafield's haematoxylin, and counter-stained with eosin or with picro-fuchsin.

When placed under the microscope, it became at once apparent that the structure under study was not of nervous tissue, but appeared as an enormous development of the pial covering of the brain. In some of the sections there appeared to be a cavity, but this proved to be nothing more than a very large central blood vessel or sinus. In the section drawn (pl. 10, fig. 1) the true pia mater is indistinctly differentiated from the gland across the dorsum of the fourth ventricle and is fused with it. Where the pia mater curves down over the side of the

medulla, however, the tissue of the gland is continued into it as shown in the region marked "A" in plate 10. As stated above, there is no apparent differentiated covering of the gland.

Of the various histological elements present, the most conspicuous are the extremely large and irregular, black pigment cells, scattered irregularly throughout the whole organ. These cells are similar to those in the pigmented covering of the brain, except that they are not so flattened, and send their branches freely in all directions. Under the high power of the microscope, they show the typical granular structure of melanin pigment cells, and the granules are often somewhat scattered at the periphery, where the cell has been cut. Some of these pigment cells measure fully eighty microns from tip to tip of their branches.

In the middle of the dorsal part of the gland there is an open reticulum of connective tissue which is gradually encroached upon by the more solid substance (pl. 10, fig. 1). From the microscopical appearance of other parts of the gland, there is much evidence that this reticulum forms the framework for the entire structure, the other elements being netted in it. The appearance of this network in a "solid" part of the gland may be seen in plate 11, figure 2, which represents such a portion highly magnified. Farther cephalad than the region shown in plate 10, figure 1, which represents a section slightly in front of the middle, the network becomes more and more open, until, on the sides under the cerebellum, nothing is left but the reticular connective tissue with a few pigment cells in it. Blood vessels are of frequent occurrence, running in all directions, and ranging from very large ones visible to the naked eye to very minute capillaries. Even in the open network of connective tissue surrounding the hinder part of the cerebellum, and constituting the cephalic portion of the structure in question, blood vessels ramify quite freely. The pia mater on the sides of the medulla, and surrounding the cerebellum, is almost a solid mass of blood vessels, which are densely crowded with corpuscles, so crowded, in fact, that they appear as solid masses of tissue, and their identity was for some time in doubt. Caudally, the open network of connective tissue is lost entirely, and the gland appears solid throughout, and denser than the portion drawn (pl. 11, fig. 2).

The histological elements found in the connective tissue network of the gland, in addition to pigment cells, are of three kinds: (1) large, clear cells with small, deeply staining nuclei (pl. 11, fig. 2, *eryth.*) ; (2) large cells more or less deeply clouded with blue in material stained in haemotoxylin, and showing evidence of reticular chromatin network (pl. 11, fig. 2, *leuc.*) ; and (3) cells filled with masses of granules staining deep red with eosin, and yellow with picro-fuchsin (pl. 11, fig. 2, *gran. m.*).

The first cells above mentioned seem to be erythrocytes, as they have precisely the same appearance as those filling the vessels in the pia mater, where they are associated with fairly numerous leucocytes. They are scattered freely throughout the gland, entirely independent of vessels of any sort. This is very remarkable for an animal which has a closed blood system, and no explanation for such a phenomenon, if they really be erythrocytes, has yet been found. These cells range from eight to ten microns in diameter, are clear and transparent, with small, round, deeply-staining nuclei, and are irregular in outline; though this may be due to slight shrinkage or contact with other cells.

The second cells above described have much the appearance of large leucocytes. They are very uniformly round in outline, and vary from seven to nine microns in diameter.

The most peculiar and characteristic element present, however, are the numerous cells filled with granules. The granules are about one and a half microns in diameter, and are very nearly the same in size as the melanin granules in the pigment cells. Where a pigment cell and a mass of granules have been cut in close proximity and both types of granules slightly scattered, it is difficult to distinguish them except by color. As stated above, they stain a very deep red with eosin, suggesting eosinophile granules in leucocytes, but they are larger and occupy the cell more completely, as figured by Rawitz (1900). With picro-fuchsin, on the other hand, they stain a deep yellow, similar to the color given to muscle fibres. In many of the vessels of the gland, especially in the larger ones, there are areas filled with a substance which strongly suggests granules in process of disintegration, and occasional scattered granules still intact may be

found in these areas. It is further significant that the substance stains exactly the same as the granules, red with eosin, and yellow with picro-fuchsin. I cannot say that the granules do pass into the vessels and disintegrate, but there is no positive evidence against it, and there are some facts in favor of it. Although the granules appear to be normal, the possibility exists that they may be due to parasitism, or some other abnormality.

The masses of granules, from ten to twelve microns in diameter, are held together by some membrane, probably a very thin cell wall, but it is not evident in the sections. The granules are sometimes scattered somewhat when the mass is cut across just as are the melanin granules in the pigment cells. Associated with each mass there is a fairly large nucleus which shows much more plainly in some cases than in others (pl. 11, fig. 2). Due to the lighter coloring of the granules with picro-fuchsin, the nuclei show best with that stain. These granular masses are found in varying density throughout the gland, except in the open connective tissue network immediately behind and around the cerebellum. In the main body of the gland they are scattered in approximately the density shown in plate 11, figure 2, though possibly on an average slightly more numerous. In the ear-like projections, however, they are far more dense, so dense, in fact, as to obscure all the other kinds of cells, and to conceal the reticular network entirely.

DEVELOPMENT

Thinking that the origin and development of this gland-like structure might throw some more definite light on its nature and function, I sectioned a series of embryos ranging from 6 mm. to 22 mm. in length. The heads of these embryos were stained *in toto* in Delafield's haemotoxylin, imbedded in paraffin, and cut in sections 10 microns in thickness.

As the eosin counter-stain was the most effective with the adult, this was likewise used for the embryos.

Up to the 18 mm. stage there could be found no indication whatever of any structure lying over the myelencephalon, the ependymal lining of the brain cavity coming in close juxtaposition to the cartilaginous roof of the skull, or lying immediately

beneath the skin in the very young specimens in which the cartilaginous roof is not yet developed.

In the 18 mm. specimen was found the first indication of any tissue intervening between the brain covering and the roof of the skull, in the form of a blood sinus, a space across the dorsum of the myelencephalon filled with blood corpuscles. In the 21.5 and 22 mm. stages the condition is very similar except that the blood sinus is larger and more conspicuous. A typical section through the myelencephalon of the 21.5 mm. embryo is shown in plate 12, figure 3. Between the band of columnar endothelial cells covering the fourth ventricle, and the cartilaginous roof of the skull, there is a space largely filled with blood corpuscles, and with a few strands of reticular connective tissue. A few scattered pigment cells may also be seen. Immediately beneath the skin, even in those embryos where the roof of the skull is not yet developed, there is a dense layer of pigment cells. As the cartilage grows over the dorsum, it is easy to see how some of the pigment cells might be pinched off and left inside, there to multiply and cause the apparently useless pigmentation of the covering of the brain. At any rate, it seems highly probable that the pigment cells found there are derived from the pigmented layer of the integument.

The next embryo available for study was a 55 mm. specimen which was cut in sections 10 microns in thickness and stained with Delafield's haemotoxylin and erythrosin. The condition there presented is extremely instructive, as it is in every way intermediate between the 22 mm. stage and the adult form. The space between the covering of the fourth ventricle and the skull is much widened, being at least as wide as the depth of the fourth ventricle. This space is largely empty, but is partially filled by a reticulum of connective tissue (pl. 12, fig. 4). In this reticulum are large blood sinuses, more or less densely crowded with corpuscles, and with a number of large, scattered pigment cells. The latter differ from those in the adult structure in that they are far more regular in outline, often nearly round, and without the dendritic branches displayed later. It will be noticed that in plate 12, figure 4, there are lateral outpocketings of the ependymal epithelium. Farther caudad these outpocket-

ings are larger and much more pronounced, curving forwards or backwards, so that in some sections they appear entirely separated from the ependyma, and look like cavities lined with epithelium and surrounded by the reticular connective tissue lying over the myelencephalon. Farther caudad than the region represented in plate 12, figure 4, also, the cavity over the brain is much extended laterally, and the lateral portions are largely filled in with embryonic connective tissue cells. These regions seem to be the centers of proliferation of the connective tissue, as here the cells are hardly differentiated, while towards the median line the reticular processes of the cells become more and more developed, and the cells themselves become fewer in number. At this stage the gland has not the definite outline which is apparent in the adult, and there is still no indication of the leucocytes or granular masses which form such a conspicuous part of the fully developed structure.

It has not been possible thus far to obtain a specimen intermediate between this 55 mm. stage, and a young adult of 250 mm., the brain of which is figured entire in figure A. This specimen has not yet been sectioned, but as it is adult in all characters except size, it is doubtful whether it will throw any more light on the development of the gland. It has, in this specimen, the characteristic shape, but is slightly smaller in proportion to the brain than in older individuals.

SUMMARY

1. A lymphoid, gland-like structure overlies the myelencephalon of *Lepisosteus*, and is closely associated with the pial covering of the fourth ventricle. Though large and conspicuous, it has been almost universally overlooked by workers on the brain of *Lepisosteus*.

2. The myelencephalic gland (provisionally so named) is present in both *Lepisosteus osseus* and *L. platostomus*, which are the only species of the genus examined by me. No indication of it has been found in other ganoids.

3. The size and form are very constant in all specimens dissected and are practically the same in both species. Topographically it seems to be a highly developed portion of the pia mater.

4. The microscopic structure is suggestive of a lymph gland. A reticulum of connective tissue underlies the whole, and in this a number of other histological elements are netted.

5. The most characteristic feature is the abundance of cells containing masses of granules staining deeply with eosin, of unknown nature, and resembling melanin granules in size and form.

6. There is some evidence that the granules mentioned above pass into the blood vessels and there disintegrate.

7. The earliest indication of the structure is in an 18 mm. embryo, where there is a blood sinus lying between the covering of the fourth ventricle and the cartilaginous roof of the skull. This sinus is larger and more conspicuous in embryos 21.5 and 22 mm. in length.

8. In a 55 mm. embryo the condition is directly intermediate between the 22 mm. stage and the adult. The connective tissue reticulum and pigment cells are well developed, and large blood sinuses are still present, but the granular masses so characteristic of the adult are not yet in evidence.

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EXPLANATION OF PLATE 10

Fig. 1. Cross-section of the myelencephalon and myelencephalic gland of a *Lepisosteus osseus*, 250 mm. in length. Section taken slightly cephalad of middle of gland, and cut farther cephalad on right than on left. $\times 12$.

ABBREVIATIONS

A—region where tissue of gland extends into pia mater.
4th vent.—fourth ventricle.
bl. ves.—blood vessel.
col. c.—columnar epithelial cells.
conn. tiss. n.—connective tissue network.
d. gran. m.—region dense with granular masses.
endol.—endolymph.
fl. c.—flattened epithelial cells.
inf. pl.—infolding of choroid plexus.
med.—medulla oblongata.
nerv.—nerve.
pig.—pigment cell.
p. m.—pia mater.

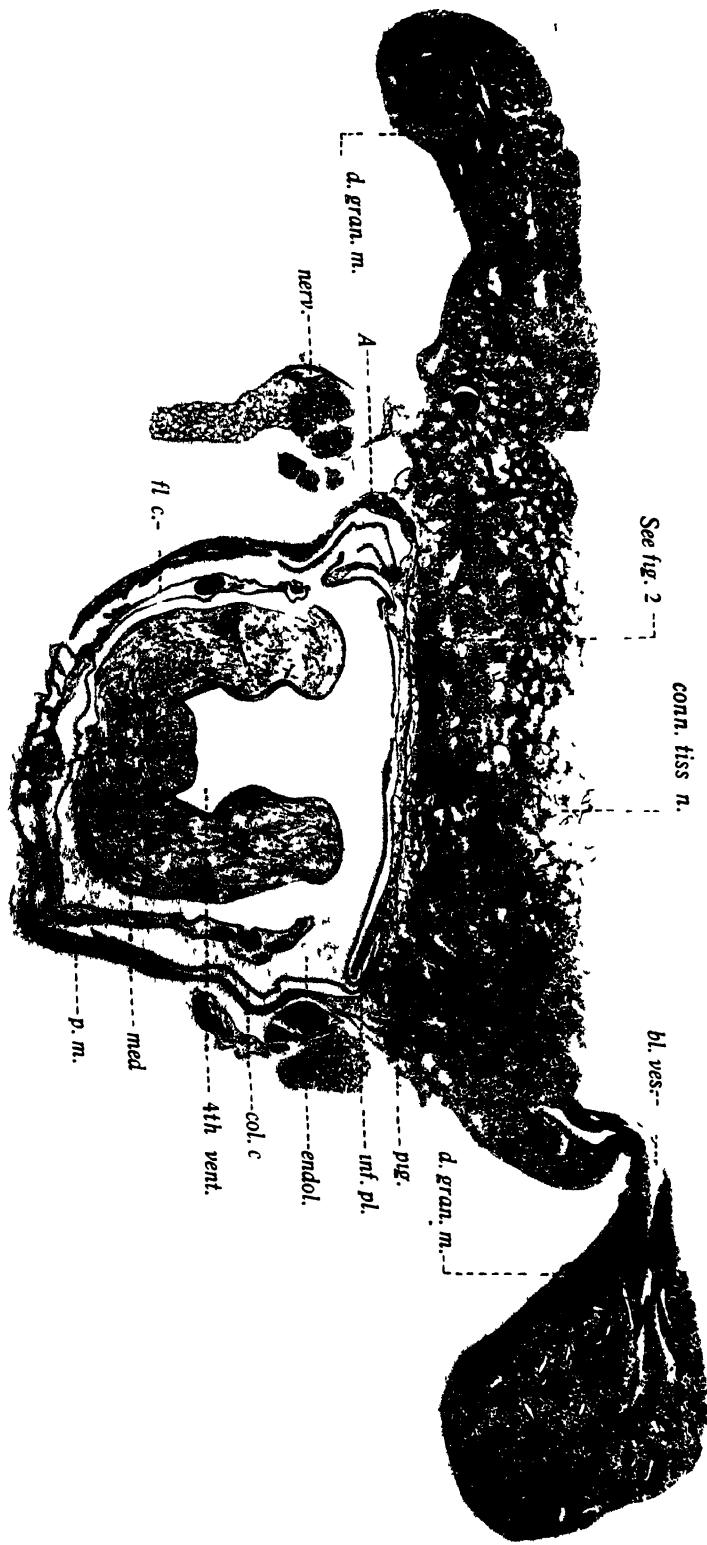


PLATE 11

Fig. 2. Highly magnified portion of myelencephalic gland of *Lepisosteus osseus* from region marked with circle in figure 1. $\times 764$.

ABBREVIATIONS

conn. tiss. n.—connective tissue network.

eryth.—erythrocyte?

gran. m.—granular masses.

leuc.—leucocyte?

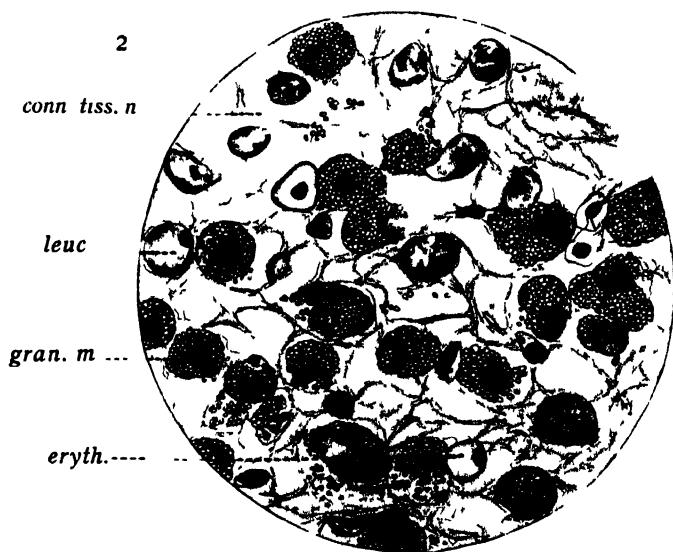


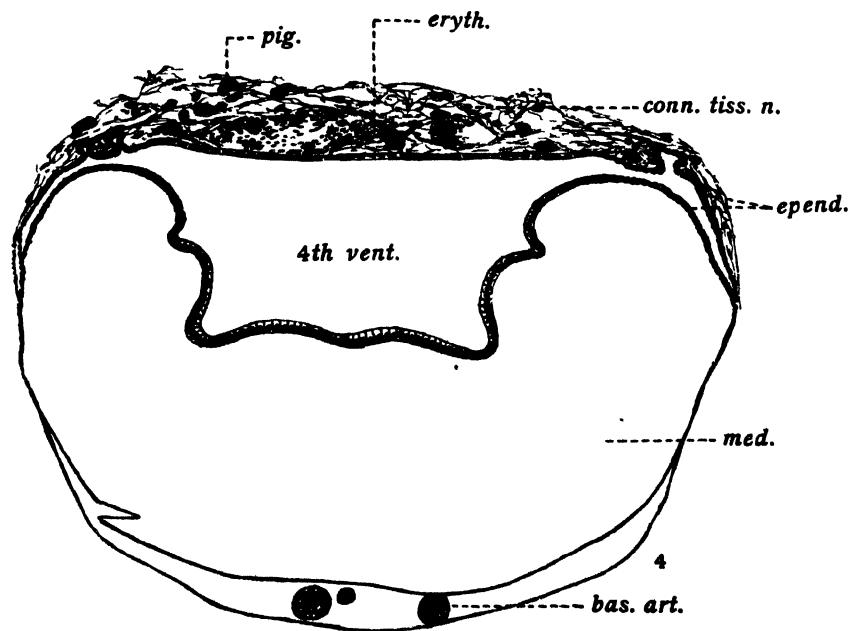
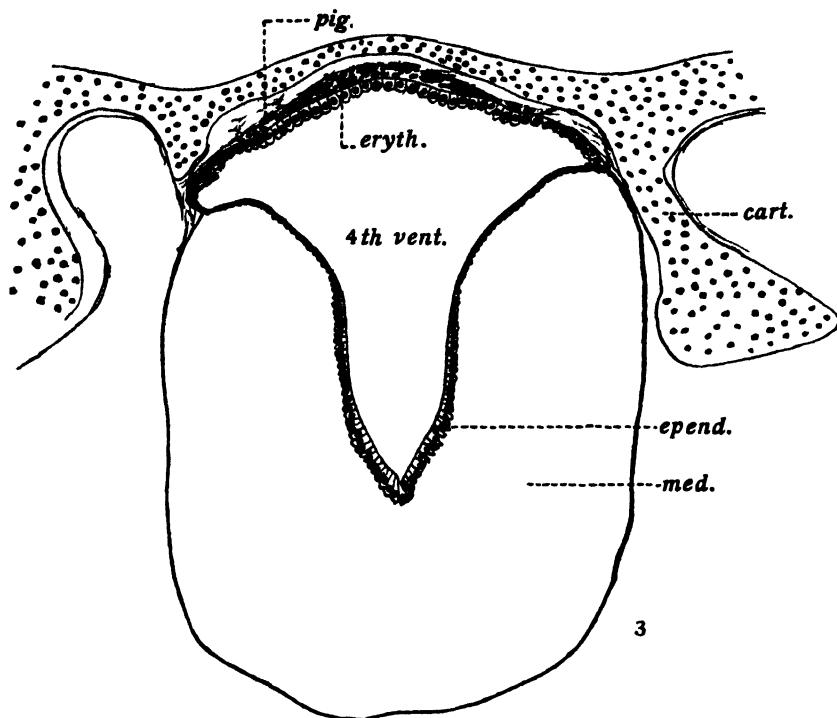
PLATE 12

Fig. 3. Cross-section of myelencephalon of 21.5 mm. embryo of *Lepisosteus osseus*, showing "anlage" of myelencephalic gland. $\times 112$.

Fig. 4. Cross-section of myelencephalon of 55 mm. embryo of *Lepisosteus osseus*, showing further development of myelencephalic gland. $\times 85$.

ABBREVIATIONS

bas. art.—basilar artery.
bl. sin.—blood sinus.
cart.—cartilage.
conn. tiss. n.—connective tissue network.
epend.—ependyma.
eryth.—erythrocytes.
med.—medulla oblongata.
pig.—pigment cell.
4th vent.—fourth ventricle.



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STUDIES ON EARLY STAGES OF DEVELOPMENT IN
RATS AND MICE. No. 3

BY

E. L. MARK AND J. A. LONG

THE LIVING EGGS OF RATS AND MICE
WITH A DESCRIPTION OF APPAR-
ATUS FOR OBTAINING AND
OBSERVING THEM*

(*Preliminary Paper*)

BY

J. A. LONG

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* No. 1 of these studies is Long and Mark, "The maturation of the egg of the mouse," Publ. Carnegie Inst. Wash., 1911. No. 2 is Mark and Long, "Die Reifung der Eier der Maus," Verh. 8, Intern. Zool. Kong., Graz, 1910.

INTRODUCTION

The solution of the complex problems of heredity, of transmission and of sex determination requires experimental studies as well as investigations of the normal events and conditions of reproduction. It was with this idea in mind that the writers undertook the present series of studies on mammalian sex cells, the first published results of which have already appeared (Long and Mark, 1911; see also Mark and Long, 1911). At present an attempt is being made to cross rats and mice, as well as to study the course of early development in each species, both under normal conditions and also under artificial conditions which simulate natural ones as closely as possible. It is believed that a comparison of the results thus obtained, both by hybridization and independently of it, will be instructive.

The following preliminary communication (No. 3 of these studies) is the outcome of an attempt to devise methods of manipulation which will enable the experimenter more successfully to control the material under investigation, and especially to enable him to follow in the living organism the changes which are inferred from the conditions in preserved material. Further communications on the results of artificial insemination and on other problems growing out of the whole undertaking are reserved for future papers.

The present paper is the result of work done in the Zoological Laboratory of the University of California, and is a continuation of investigations carried on in the Zoological Laboratory of Harvard University, some of the results of which have been published under the title "The Maturation of the Egg of the Mouse." It is published as a contribution from the Zoological Laboratory of the University of California and also as no. 225 of the *Contributions from the Zoological Laboratory of the Museum of Comparative Zoology at Harvard College*.

The running expenses of the work have been defrayed in part from grants made by the Carnegie Institution of Washington, and in part by funds furnished through the Zoological Laboratory of Harvard University; but the special equipment required

for the present work has been supplied by the Zoological Laboratory of the University of California.

Living eggs have been studied and artificially seminated under the microscope, having been carried as far as the formation of the second polar cell. This piece of work bears only on one aspect of the larger problem we have undertaken, and although the results are at present necessarily incomplete, they are set forth with the hope that especially the apparatus devised for the problem may be of value to investigators in related subjects.

The animals used in these experiments were the ordinary white rats and mice, the ancestry of which was mixed, partly white and partly colored individuals. All were normal and in good condition.

APPARATUS

In addition to new apparatus presently to be described, some improvements have been made in the appliances used in the earlier investigation (Long and Mark, 1911).

CAGES

The cages are now made entirely of metal (pl. 13, fig. 1). They are constructed of one piece of wire netting, one-fourth inch mesh, cut into the proper shape, bent over a wooden form, soldered at the angles, and reenforced by a frame of heavy wire. In the middle is soldered a partition of the same wire netting, in which there is a hole connecting the two chambers. In the bottom of each chamber is slipped a drawer-like tray of galvanized iron, which is partly filled with sawdust or shavings and forms the floor of the cage. A sloping lid is hinged at its upper edge as shown in the figure.

BIRTH-RECORDING APPARATUS

Advantage was taken of the method of timing the birth of litters which was described in the preceding paper (Long and Mark, 1911, pp. 7-10). The apparatus is now made on the same principle, but is somewhat simplified, and is fitted with electrical contacts and magnets for marking on the chronograph drum. Figures A-C and plates 13 to 15 illustrate the construction and operation.

It will be seen that by introducing the electrical connections it is possible to have each cage, or unit for the accommodation of one animal (mouse or rat), independent of the others and also to place it in any desired position with regard to the chronograph. Three cages have been arranged to make their records on one chronograph drum. A single cage and its connections with the chronograph drum are shown in plate 15.

The following description applies to each cage or unit. The wire sides and top of the cage are supported on two uprights (*up.*, pl. 14, fig. 4), and are independent of its floor. The floor consists of two parts, each made of sheet zinc, a smaller central and a larger marginal floor. They are shown at the right in plate 13, figure 2. The larger floor (*m. fl.*, fig. A, top surface exposed in pl. 13, fig. 2) has the center cut out to accommodate the smaller; at the edges the zinc is turned up, as clearly shown in figure 2. The smaller floor (under-surface exposed in fig. 2) also has the edges turned up, but to a less extent. The smaller part, which carries the nest, fits loosely within the opening of the larger one. These two floors instead of being suspended from levers above, as in the earlier model, are supported from *below* on levers of special construction (figs. A and B and pl. 13, fig. 2). Each lever consists of a transverse bar (*tr. br.*) at right angles to which are attached three parallel bars, one (*s. br.*) projecting beyond the cage, the other two (*p. br.*, *p. br.*) terminating under the middle of the cage. The two levers are so constructed that the smaller, carrying the nest floor, occupies a position inside the larger (see pl. 13, fig. 2). The fulcrum of each lever is formed of two slender wire nails (*ful. nl.* and *ful. nl.*), which fit into slots in the sheet-metal lever supports, as clearly shown at *lr. sup.*, figure A and plates 14 and 15. The unpaired bar (*s. br.*) of each lever carries a counterweight (*wt.*); the paired bars support the appropriate floor. On the under side of each of the floors are two metal supports (fig. A, *fl. sup.*) similar to those on which the levers rest (see right hand of fig. 2, pl. 13, also pl. 14). In each support is a slot, which rides on a slender wire nail (*nl.*, fig. B) driven into the side of each of the paired bars near their free ends. Each floor thus rests on the ends of the paired bars of its lever. The floors are prevented from

tipping by means of the truss-like supports (*tr.*) attached to their under sides. To the angle of each truss is attached one end of a light bar (*lt. br.*), the other end of which is pivoted to the base board. The excursion which each lever may make is controlled by the adjustable block (*blk.*) at the end of the unpaired bar (pl. 14, fig. 3). By shifting the counterweights the

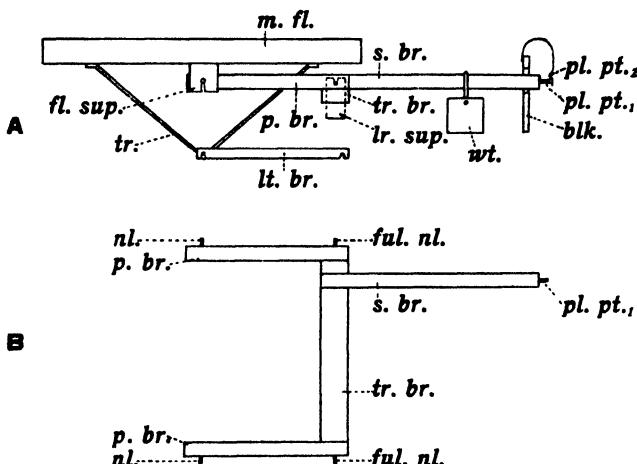


Fig. A. Diagram of side view of larger part of cage floor with its lever and accessories.

Fig. B. Plan (top view) of one lever shown in side view in figure A.

blk., adjustable block; *p. br.*, paired bars of lever; *ful. nl.*, fulcrum nail of lever; *fl. sup.*, floor support of metal attached to under side of floor and resting on slender nail (*nl.*) driven into the side of *p. br.*; *lr. sup.*, support for fulcrum of lever; *lt. br.*, light bar for steadyng floor; *m. fl.*, main floor of cage; *nl.*, nail; *pl. pt.*, *pl. pt.*, platinum points which make an electrical contact with each excursion of the lever; *s. br.*, single bar of lever which carries the counterweight (*wt.*); *tr.*, truss-like frame attached to bottom of floor to prevent tipping of floor; *tr. br.*, transverse bar of lever; *wt.*, counterweight.

floors may each be so balanced that they will be moved by a very light weight.

The movements of the floors are recorded on the drum of a chronograph by electrical means. The marking apparatus consists of two small signal magnets (fig. C), which are adapted to the purpose by reversing the position of the parts in one and removing its supporting bar. The arrangement is shown in figure C and plate 15. One end of the wire of each coil is grounded in

the supporting frame; the other end terminates in a binding post. The armatures carry slender pointers (*p.*), which mark the smoked paper of the drum. The connections with the cages are simple. Each lever of a cage actuates one of the two magnets. Attached to the outer end of each unpaired bar (*s. br.*) of the lever is a platinum point (*pl. pt.₁*) which is connected by a wire (*wr.*, pl. 13, fig. 2) with one fulcrum-nail of the lever. A movable contact is thus made between the nail and the metal lever support (*lr. sup.*), which in turn is connected through a

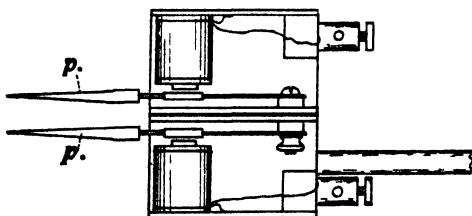


Fig. C. Signal magnets with attached pointers, which record on the chronograph drum the movements of the two parts of the floor of the cage.

binding post at *b. p.* (pls. 13 to 15) with one pole of a battery. With each excursion of the lever the platinum point at its end comes into temporary contact with another platinum point (*pl. pt.₂*) supported on the adjustable block (*blk.*). This second platinum point is connected with the binding post of the appropriate magnet (compare pl. 14, fig. 3; pl. 13, fig. 2, and pl. 15). The frame and support of the magnets is connected by a wire (*c. wr.*, pl. 15) with the other pole of the battery. Contact between the platinum points completes the circuit and the battery actuates the magnet, which pulls to itself the pointer (*p.*), and thus a vertical mark is made on the drum. Inspection of the figures will make clear these arrangements.

The working of the machine is nearly the same as in the one previously described, the important difference being that in the present machine it is possible to determine only the passage of the animal into and out of the nest, whether it be before or after a litter is born. For further details see Long and Mark, 1911.

For studying and experimenting on living eggs of mammals, apparently no suitable apparatus has ever been made. Several conditions must be fulfilled by a successful apparatus: the temperature of the microscope and accessory apparatus must be fairly constant; there must be some way of keeping the eggs that are under observation in suitable artificial media, of seminating them, and of removing the excess spermatozoa. To meet these requirements the writer has devised and constructed the two pieces of apparatus now to be described. They consist of a double-walled box, made of glass and wood, heated to a constant temperature by an automatically controlled electric current, and of a circulation slide, in which eggs can be placed for study and experimental treatment.

CONSTANT-TEMPERATURE BOX FOR MICROSCOPE

The box (figs. D to H, and pls. 16 and 17), which is large enough to contain two microscopes, a compound and a binocular, and also accessory apparatus and cultures, measures inside at the level of its floor about 30 by 18 inches, (76 by 45.5 cm.). The greatest inside height is about 11½ inches (29 cm.). The box is supported on legs. The general appearance and shape is so well shown in the photographs (pls. 16 and 17) and in the vertical sectional view (fig. D) that only a brief explanation is necessary.

As can be seen in figure D, the upper part of the box, which is the part containing the microscopes, etc., is so shaped that the operator can work near the microscope with the least inconvenience, and so that the least light is cut off from the mirror, whether by reflection from the glass of the sloping front or by the lowness of the roof.

The walls of the upper part are of heavy glass (about $\frac{1}{5}$ inch, or 5 mm. thick) except the back and ends (pl. 16 and fig. D) which are of wood, and are double except at back, where there are holes through which the hands are passed in working. The end walls are covered inside with glass plates (fig. E and pl. 17), so that the box is lined with glass save for the back and floor. Where glass plate comes into contact with glass plate one or both edges are ground perfectly straight to ensure a tight joint. Details of the construction can be seen in figures D and E. The

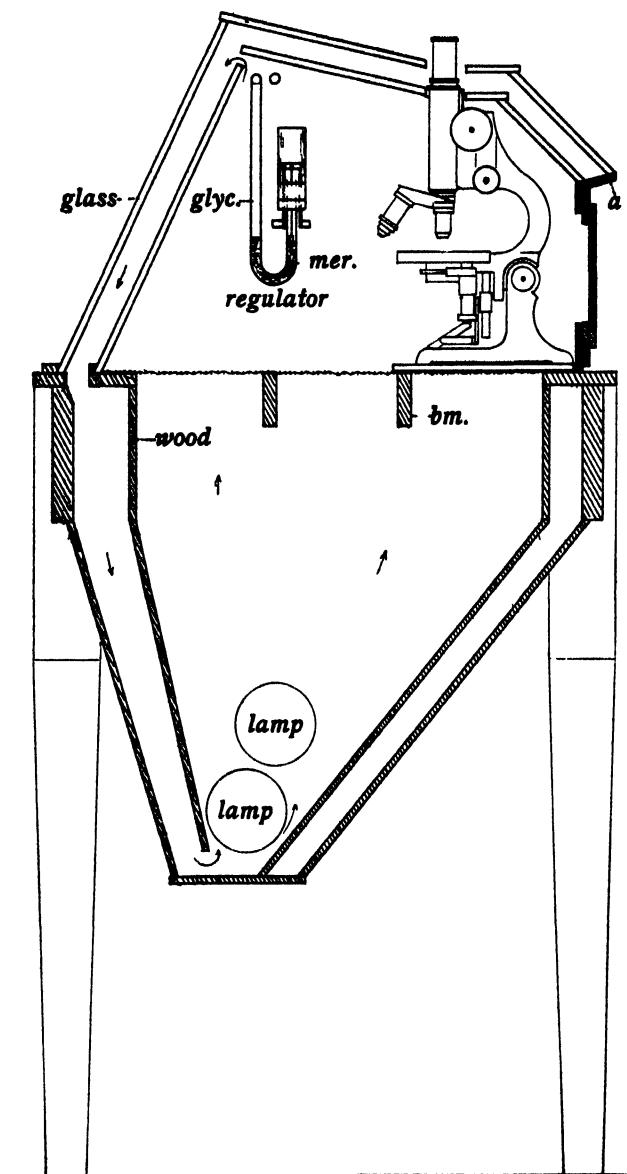


Fig. D. Transverse vertical sectional view of constant-temperature box for microscope. The regulator, which is at one end of the box and not opposite the microscope, is projected on the drawing. The air circulation is indicated by the arrows. *a*, place where cloth is attached; *bm.*, longitudinal supporting beam for wire netting floor; *glyc.*, glycerine-filled tube of regulator; *mer.*, mercury-filled U-bend of regulator. $\times \frac{1}{8}$.

three hand holes are large enough to permit the hand to pass easily. They are closed by small sliding doors; and the middle

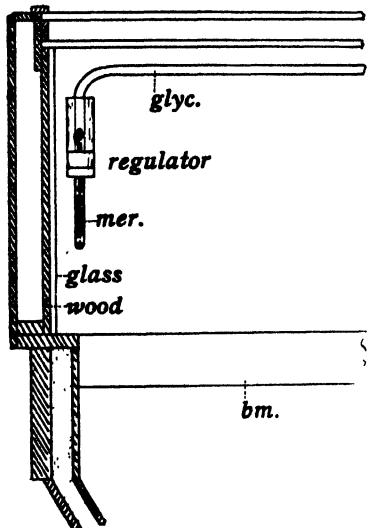


Fig. E. Longitudinal vertical sectional view of one end of the box shown in figure D. Letters as in figure D. $\times \frac{1}{4}$.

and right hand ones are cut in sliding doors, which in turn cover larger holes in the wooden back (see fig. D and pl. 16). This arrangement permits enough lateral and vertical motion of the wrists to enable the operator to reach all parts of the interior without appreciably affecting the temperature within. Several folds of cloth (omitted from the photographs for the sake of clearness), fastened along the top above the holes (a, fig. D) and hanging down over them, are very effective aids in keeping the temperature constant.

In figure D it can be seen that the microscope tubes pass

through the glass where the edges of the roof plates meet. The holes in the glass are bored so that the glass fits snugly about the tubes of the microscope. Plate 17 shows how the wooden back, a part of the wooden end walls, and all of the glass back of the microscopes, can be removed in order to allow the microscopes to be put in place or to introduce large objects.

The floor on which the microscopes and apparatus rest consists of wire mosquito netting supported at the edges and by two longitudinal beams (bm., figs. D and E) running through the middle. The microscopes rest on strips of heavy glass which lie on top of the netting, but are supported directly by the beams and at the edges. Smaller objects are most conveniently placed on pieces of glass large enough to reach from one wooden support to another.

The object of having a floor of netting is to allow the ascent of the air which is warmed in the lower part of the box below the floor. This lower part of double, wooden walls is shown in

figure D and plate 16. It has the form of an elongate, truncate pyramid, which is lined with heavy asbestos paper, and contains at its lower end the heating lamps. These are connected with a regulator to be described presently. The space between the double walls is filled with cotton, except at the front where the space communicates below with the chamber where the lamps are, and above with the space between the two plates of glass which form the front wall of the upper box. The latter space in turn is connected at the peak of the roof with the interior of the box. Consequently air warmed by the lamps rises, filters through the net floor, envelopes the apparatus, and passes out above, whence it descends between the front walls to the lamps. There is thus a constant circulation preventing the accumulation of hot air above and cold below.

The heating apparatus consists of four 32-candle power incandescent lamps arranged in two pairs. The members of each pair are connected in series. As a result they do not burn with maximum brightness and heat, and they therefore use less current. One pair is directly connected to the source of the current and burns constantly, the other pair is controlled by the regulator.

The regulator, which lies entirely within the box, is made on the plan devised by Mast (1907). The tube of the regulator is suspended at the highest part of the box. It runs lengthwise (figs. D and E and pls. 16 and 17), bending back on itself several times. At the left end (figs. D and E and pl. 17) the tube turns down, ending in a U-bend filled with mercury (*mer.*, figs. D to F). The greater part of the tube is filled with glycerine (*glyc.*), its escape being prevented by a cork stopper visible in plate 16, upper figure. The shape of the glycerine-filled part is immaterial. However, the longer it is, the thinner the glass, and the smaller the diameter, the more sensitive is the regulator. The rest of the regulator in its simplest form is shown in figure F.

On the free end of the mercury-filled U-tube is fitted a cork (*cork*). The cork is pierced by two heavy wires (*lr. wr.* and *ct. wr.*), at the lower ends of which are binding posts. The upper end of one (*lr. wr.*) is bent at right angles (figs. G and H) and passes through one end of a short lever (*lr.*) made of a piece of

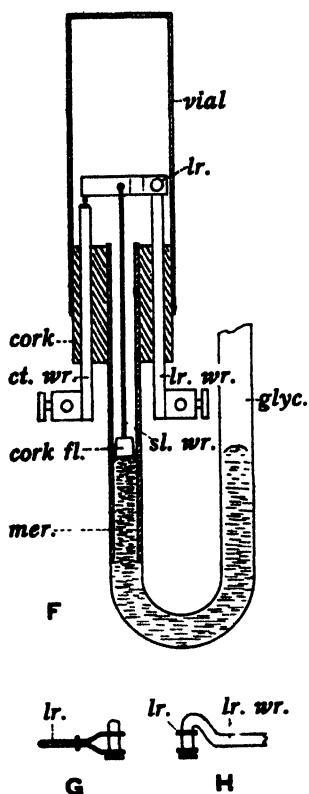


Fig. F. Diagram of thermo-electric regulator used in the constant-temperature box. Only a part of the glycerine-filled tube (*glyc.*) is shown, the rest may be seen in plates 16 and 17. $\times \frac{1}{2}$.

Figs. G and H. Top and end views, respectively, of the lever. $\times \frac{1}{2}$.

cork fl., cork float; *glyc.*, glycerine-filled tube; *lr.*, lever attached to upper end of *lr. wr.*; *sl. wr.*, slender wire between lever and float; *mer.*, mercury-filled U-tube; *lr. wr.*, *ct. wr.*, heavy wires carrying at their lower ends binding posts and at their upper ends the lever and platinum contacts respectively; *vial*, glass vial.

sheet copper shaped and bent as shown in figures F, G and H. At the free end of the lever is soldered a bit of platinum wire, which may touch a small plate of platinum soldered to the upper end of the other heavy wire (*ct. wr.*) and thus make an electric contact. At the middle point of the lever a small hole receives one end of a straight piece of slender wire (*sl. wr.*), which hangs down into the regulator tube. The wire terminates in a piece of cork, which fills the tube, but without sticking or binding, and rests on the surface of the mercury. The lever and opening into the regulator tube may be protected by an inverted shell vial (*vial*) fitted snugly over the cork (*cork*). The regulator is connected in series with one pair of lamps. It can easily be adjusted for a particular temperature by slipping the cork (*cork*) up or down on the tube. The operation of the regulator depends on the expansion of the glycerine when heated. It will easily be seen that when the glycerine expands the mercury is forced down one arm of the U and up the one containing the cork float, which is thus lifted; this breaks the contact at the platinum points, thereby shutting off the lamps.

There are a few precautions which should be observed. Too strong a current through the regulator is apt to cause the points to stick slightly, thus causing a variation in temperature. This can be avoided by using

a relay or similar apparatus for carrying the heavy current. Again, in filling the tube with glycerine care should be taken to prevent glycerine from entering the part of the bend where the cork float rests on the mercury, for it is exceedingly difficult thoroughly to dry the mercury if once wet. All rubber must be avoided in order to prevent tarnishing of metal and consequently poor contacts. With proper care and experiment it is possible to keep the temperature constant to within about one-tenth of a degree centigrade.

In a large box without artificial circulation the temperature in all parts is not exactly the same, though very nearly constant. The microscope is usually a degree or so colder, apparently because of radiation from the exposed part. Accordingly the upper exposed end should be insulated with a good non-conductor, as shown in the photographs. The covering was removed from the binocular in order to make the figure clearer.

Since a camera lucida cannot be used in the ordinary way, it was found practicable, and most convenient, to remove the mirror from the camera and to use instead a large mirror supported over a small shelf at one end of the box (pls. 16 and 17). Although the magnification is greater, because of the increased distance of projection, the method is still satisfactory.

CIRCULATION SLIDE

The circulation slide of glass, perhaps the most important piece of apparatus (now being made by the Spenceer Lens Co., of Buffalo, N. Y.), is shown in detail in figures I to L and can also be seen in plates 16 and 17. The unassembled parts, placed however in their relative positions, are represented in figure I, the slide put together is seen in longitudinal section in figure J, and as set up on the stage in figure L.

The complete slide consists of several parts, shown in figure I. (1) A polished lower slide (*lr. sl.*) of glass, one inch by three, and about $\frac{1}{16}$ inch thick, is perforated by two bolt-holes (*bolt hl.*), which on the under side are countersunk to receive the heads of two short bolts. (2) A second polished upper slide (*up. sl.*), of the same dimensions as the lower and with corresponding bolt-holes is the most important part of the apparatus, being the one

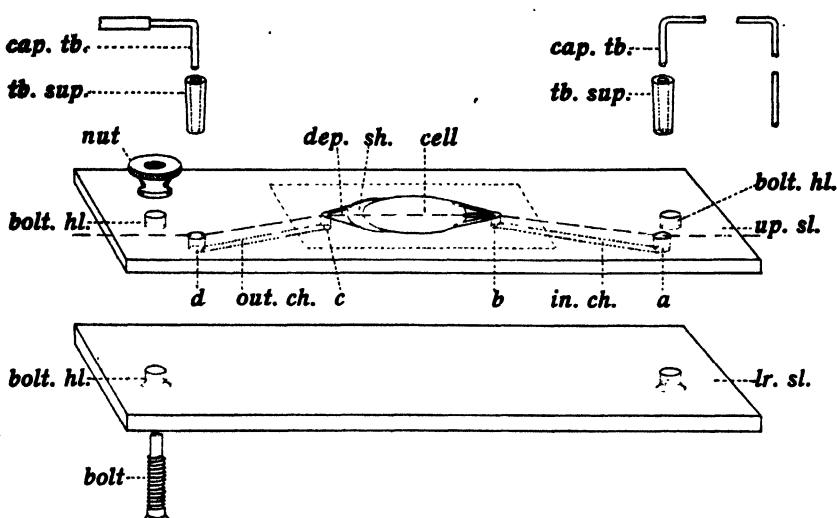


Fig. I. Assemblage of parts of circulation slide in position ready to be put together. $\times 1$.

a, d, holes which receive the tube supports (*tb. sup.*) ; b, c, holes which connect the incurrent and outcurrent channels with the cell on the upper side of the slide; *bolt hl.*, bolt hole; *cap. tb.*, capillary tube; *dep.*, depression; *in. ch.*, *out. ch.*, incurrent and outcurrent channels; *lr. sl.*, lower slide; *sh.*, shelf; *tb. sup.*, tube support; *up. sl.*, upper slide.

in which are ground and polished the cell in which the objects for study are placed, and the channels through which the fluids are conducted to and from the cell. The cell is a circular, flat-bottomed depression about 130 microns deep and 13 mm. in diameter, ground and polished in the center of the upper side of the slide. At its margin the floor is broadly rounded (figs. J and L). At one end of the cell a crescent-shaped area of the surface of the slide is ground down and polished so that it forms a shelf (figs. I, J and L, *sh.*) about 35 microns lower than the upper side of the slide and about 100 higher than the floor of

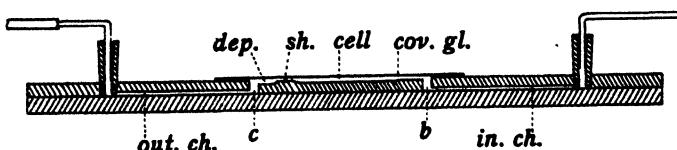


Fig. J. Longitudinal section of circulation slide taken along the dash line in figure I. $\times 1$.

cov. gl., cover-glass; other letters as in figure I.

the cell. Just outside the shelf a triangular deeper depression (*dep.*) is ground in the glass. At the outer angle of the depression a small hole (*c*), about 1 mm. in diameter, is bored through the glass and is connected by an outlet channel (*out. ch.*) or groove ground in the under side of the slide with another larger hole (*d*) leading to the upper side. At the opposite end of the cell three small grooves lead from the cell to a hole (*b*) which is connected by an inlet channel (*in. ch.*) with the hole *a*. The inlet and outlet channels on the under side of the slide are closed when the two slides are bolted together. Similarly the depression, shelf, cell and grooves on the upper side are closed when a cover-glass is placed in the position indicated by the coarse dotted line. Perfectly tight joints are ensured by thin films of vaseline encircling the inlet and outlet channels below and the cell and connected parts above. All parts are easily accessible for cleaning. (3) Fluid is conducted to the slide by means of glass capillary tubes (*cap. tb.*) and from it by both glass and rubber tubes. The capillary tubes are supported and connected with the slide by two tube-supporters (*tb. sup.*) made of short, thick-walled, tapering tubes of glass. The latter are ground into the holes *a* and *d* and fit firmly and tightly. As they do not extend entirely through the slide (see fig. J), they freely communicate with the inlet and outlet channels. All joints of the tubes, while very nearly tight, may be made completely so with bits of melted parafin.

The inlet capillary tube is dipped into a bottle, as shown at the right in figure K; the outlet tube is connected with a waste bottle by a small rubber tube which passes through a pinch-cock. The air of the waste bottle may be exhausted through another tube which passes out through a hole in the back of the box (pl. 16), and a current of fluid caused to flow through the cell. By having the waste bottle lower than the supply, the current once established becomes continuous, as a siphon, and may be accurately regulated by the pinch-cock. The glass must be chemically clean in order that the fluid may be started through without leaving air bubbles behind. Something of the arrangement of the slide and the accessory parts can be seen in plates 16 and 17.

It will easily be seen that fluid after entering the cell can

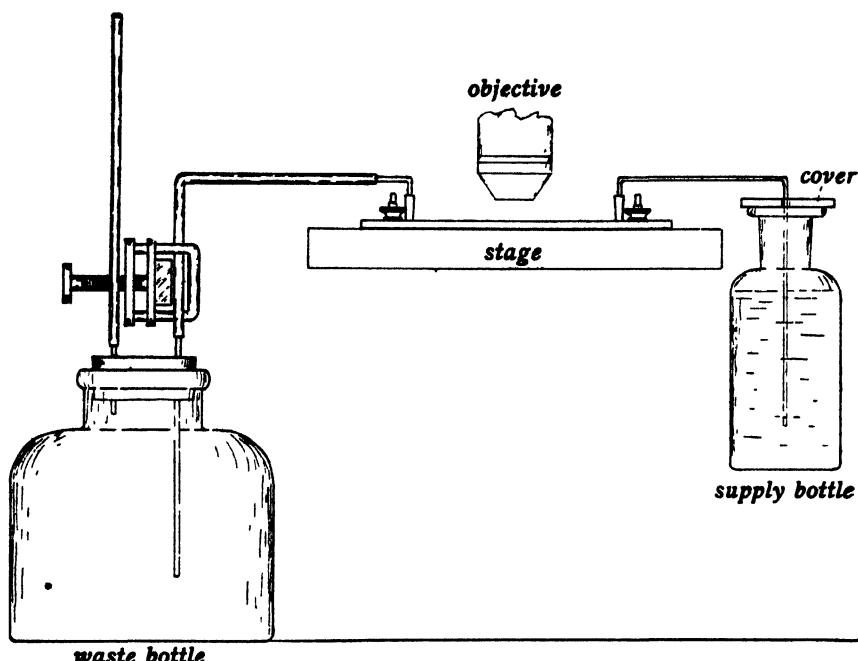


Fig. K. Circulation slide in position on stage of microscope under an objective and connected with supply and waste bottles. The supply bottle is covered by a perforated glass cap; it is supported on a circular disc shown in plates 16 and 17. $\times \frac{1}{2}$.

escape only through the narrow space above the shelf (*sh.*), which is shown in the enlarged sectional view of the outlet end of the cell (fig. L), while objects of large enough size are retained in the cell. Thus mammalian eggs are held back by coming into

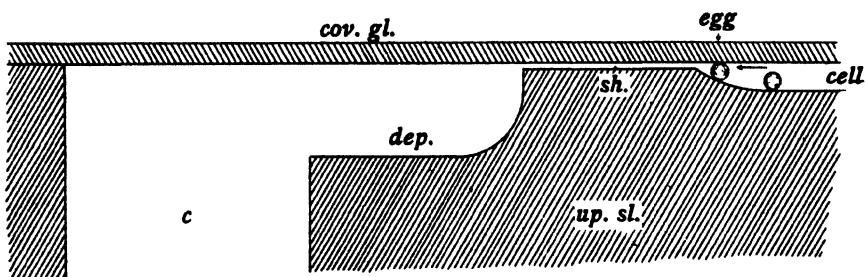


Fig. L. Semi-diagrammatic longitudinal section through part of the upper slide (*up. sl.*) at the outlet end of the cell; i.e., through part of the cell, the shelf (*sh.*), the depression (*dep.*) and hole (*c*) shown in the figures I and J. Cover-glass (*cov. gl.*) above. $\times 25$. It shows two eggs and the way in which one is being prevented from being washed away by the current which passes from right to left.

contact with the curved floor of the cell below and the cover-glass above. The current, if strong enough, causes a slight flattening of the eggs, but can be so regulated that the eggs are held without distortion against the under side of the cover-glass. Under such conditions they may be studied with an oil immersion lens.

A slide such as the one just described can easily be modified to make it available for many kinds of cultural and experimental work, whether with gases, fluids or electric currents. It can also be used for fixing and staining under the microscope.

For convenience in quickly changing the fluids to be passed through the slide a number of small glass stoppered bottles are supported (by having their necks let into slots) on the rim of a circular wooden disc, which may be both rotated about a vertical axis and also raised or lowered on the central shaft. Plates 16 and 17 show the bottles as they are used, and figure M is a vertical section showing the construction of the parts supporting the disc. The rod (*rd.*) has along one side a groove (*gr.*), in which a pin (*pin*) of the sleeve (*sl.*) fits. The sleeve has at its lower end a flange, which rests on a spiral spring and

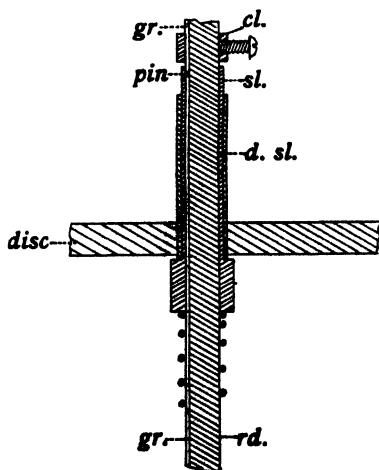


Fig. M. Section of metal supporting parts of the center of disc for holding reagent bottles. $\times \frac{1}{2}$.

cl., collar and set-screw; *disc*, wooden disc; *d. sl.*, metal sleeve to which disc is attached; *gr.*, groove; *pin*, pin; *rd.*, central supporting rod; *sl.*, sleeve resting on spiral spring and about which the sleeve (*d. sl.*) may rotate—it may move vertically, but is prevented from rotating by the pin.

in turn supports above a second tube or sleeve (*d. sl.*), to which the disc (*disc*) is attached. This arrangement allows free rotation of the disc and prevents any torsion in the spring being communicated to the sleeves. But for this, the disc might turn back and break the capillary tube which passes from the slide into the bottle. A collar (*cl.*) with set-screw determines the greatest height at which the disc is supported by the spring. In preparation for changing the fluid in the slide it is only necessary to depress the disc, rotate it until the desired bottle is in place, and then allow the spring to raise it so that the capillary tube passes into the bottle.

When one fluid is to be used for some time, evaporation from the bottle is greatly reduced by having the upper end of the neck ground perfectly flat and covering it with a piece of a polished glass slide (*cover*, fig. K). This cover is perforated by a hole just large enough to admit freely the capillary tube. As the slide on the stage of the microscope is moved about by the mechanical stage the cover slips over the polished surface of the neck.

OBSERVATIONS

Eggs for study were in all cases obtained from the oviducts. Knowing that in mice ovulation occurs fourteen or more hours after parturition, it is only necessary to know when a litter is born and to kill the female fourteen to seventeen hours later. Out of fifteen mice killed for live eggs, seven, killed on the average 16.2 hours, and two, killed 24 and 25 hours, respectively, after parturition, contained eggs in the oviducts. In two other cases the exact time was not known. In the four cases in which eggs were not found the average time was 19.9 hours. In successful cases the eggs were easily visible in a fold of the oviduct near the ovary. Previous work on fixed material demonstrated that soon after ovulation the eggs are in the above fold of the oviduct, where they lie in a cluster surrounded by corona or follicle cells, and that later, as they pass along the oviduct, they become separated and lose the enveloping follicle cells. Study of live material abundantly substantiates the earlier findings, for the cluster of eggs and follicle cells can be identified through the

thin transparent distended wall of that part of the oviduct. In the unsuccessful cases discharged follicles apparently were present in the ovary, but there were no eggs in a cluster in the oviduct. It is probable that they were isolated and naked and hence escaped observation. The search (for scattered eggs) is further made difficult by the secretions in the oviduct, the presence of follicle cells, some blood corpuscles and fat droplets, and also by the rapid drying of the minute oviducts.

Out of thirteen rats used for obtaining live eggs, ten, killed on the average 18.7 hours after parturition, furnished eggs in the oviduct. The other three, in which none could be found, averaged 20.2 hours. Failure can probably be explained here as a result of conditions as in the case of mice, although fixed material has not been studied. There is thus a comparatively very short period during which eggs are procurable. If the animal is killed too soon, the ova will not have had time to leave the ovary; if too late, the eggs will have passed on through the oviduct and escape even careful scrutiny.

In regard to ovulation in rats, it will be seen from the data just given that it must occur on the average less than eighteen hours after parturition.

In the case of both mice and rats the method of procuring eggs was as follows: the animal when killed (mice by breaking the neck, rats by cutting the spinal cord between the cranium and atlas) was quickly opened, one ovary and oviduct removed to the stage of the binocular in the constant-temperature box and placed on a clean, sterile cover-glass of the proper size. When the fold of the oviduct containing the eggs was found, it was moved to the middle of the cover-glass, cut, and the cluster of eggs allowed to flow out. The cluster is jelly-like and highly translucent. The eggs being protected by the follicle cells, the slight drying serves to make them adhere to the cover. A drop of Ringer's fluid, or in a few cases, blood serum, was placed over the eggs, and the cover-glass inverted over the cell of the slide. Up to this point the manipulations required from five to fifteen minutes. When the slide was connected by the glass tubes with the waste and reagent bottles, the chamber was easily filled with the desired fluid. With care nearly all air could be

driven out, for the eggs at first withstand a violent current without becoming detached.

Spermatozoa are easily introduced into the chamber after mixing them with a few drops of Ringer's fluid. Unfortunately for clear observation the eggs, especially those of the rat, are greatly obscured by the follicle cells, and thus far the penetration of the spermatozoon into the egg has not been observed.

The immediate effect of the spermatozoa is not quite the same in all cases. Mouse spermatozoa are exceedingly active in the salt solution. In one experiment they had within two minutes thrashed the follicle cells loose, and bared the eggs, which they then kept in rapid rotation. Usually the follicle cells are loosened less violently, becoming scattered within twenty to forty-five minutes. It is then possible to wash out the excess of spermatozoa and the follicle cells, leaving the eggs quite free in the chamber of the slide. By judiciously pinching the rubber tubing leading to the waste bottle the eggs may be moved about and freed from debris. While most of the spermatozoa when first introduced became attached to follicle cells and lashed the water violently, a number penetrated between the follicle cells and moved about with a slower sinuous motion, strikingly like that of a free-living nematode. The latter sort of motion is more effective, for the spermatozoa exhibiting it progress much more rapidly with the same amount of activity. Presumably this is the way they move up the uterus and oviduct.

At first scarcely anything can be observed of the zona pellucida. However, after the eggs are freed of the follicle cells in Ringer's solution, the zona is clearly visible as a highly transparent, thick envelope. In blood serum the zona is invisible. It is not closely applied to the egg, from which it is sometimes separated by a considerable space, especially in the region of the first polar cell. Sometimes the first polar cell seems hardly to touch the egg, again it lies in a slight depression in the surface of the egg.

The cytoplasm of the eggs of both mice and rats is beautifully transparent, so clear that it is possible to see distinctly granules at the lower pole. In both there is a granular ingredient, though it is different in the two ova. In eggs of mice

the granules are apparently single or in clusters of various sizes pretty uniformly distributed. They seem, under an oil immersion, to be more or less angular. In eggs of the rat, on the other hand, the granules are not so clean cut and brilliant, and before maturation is complete they are arranged irregularly. The egg has a somewhat mottled appearance, as though the granules formed a very coarse network. After the second polar cell is formed, this appearance is lost and the distribution of the granules is quite uniform.

Nothing whatever can be seen in the living egg of nuclear or spindle figures.

The eggs of both animals are approximately of the same size. Since salt solutions of slightly different density cause variations in the size of the eggs exact figures cannot now be given.

The first polar cell of the mouse egg was present in most of the eggs observed. It is large and very conspicuous and its cytoplasmic contents are very similar to the egg cytoplasm. It is more or less spherical, sometimes flattened, at times clearly amoeboid, lightly in contact with the egg or situated in a slight depression in the surface of the egg. The amoeboid condition may well account for the change in position described by several writers. When fixed, the zona is caused to contract quickly into contact with the cytoplasm and the polar cell to be rather deeply pressed into the egg. No second polar cell has so far been formed under the microscope, even when active spermatozoa are introduced into the artificial fluid.

In the rat the first polar cell is much less conspicuous. It is smaller and may easily be overlooked.

It has been possible to seminate rat eggs with rat spermatozoa and to observe the formation of the second polar cell. Fortunately the eggs always lie in such a position that the forming polar cell can be seen in profile. The formation, usually near the first polar cell, may begin within five minutes to two or more hours after the spermatozoa are introduced. The constriction may be finished three-fourths of an hour later. The process is strikingly like that described (Long and Mark, 1911) for the mouse egg as far as the external features are concerned. The first appearance is an elevation clearer than the rest of the

egg. The swelling becomes higher and at one side of the elevation there appears a depression which is the beginning of the constriction which presently encircles the whole swelling and cuts it off from the egg. The polar cell is at first clear, as in the mouse, and later becomes granular like the egg cytoplasm. There is at one side of the polar cell on the surface of the egg a temporary elevation, for which at present I have no explanation.

While the second polar cell is at first spherical, it becomes irregular and distinctly amoeboid, undergoing, perhaps amitotically, division into unequal parts. It seems to degenerate, growing smaller and more granular.

At present nothing can be said as to the changes which the chromatin undergoes after the spermatozoon has penetrated the egg.

The egg itself becomes more nearly spherical after the second polar cell is abstracted.

The eggs remain alive and apparently normal for about twelve hours, when they begin to degenerate, the outlines growing ragged, the granular contents becoming dull and contracted toward the center, leaving a clear peripheral zone. The causes are not at present determined. In some cases bacteria play a part.

No reason can at present be assigned for the failure of mouse eggs to produce a second polar cell; nor can the precise conditions under which it is formed in rat eggs be set down. Therefore a further discussion at present is not desirable.

Zoological Laboratory, University of California.

Transmitted July 28, 1911.

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EXPLANATION OF PLATES

PLATE 13

Fig. 1. All-metal cage for mice or rats.

Fig. 2. Top view of cage and apparatus for recording automatically the time of birth of litters of rats or mice. The floors are removed and are seen at the right, the larger from above, the smaller (which carries the nest, an inverted strawberry box, see pl. 14) from below.

ABBREVIATIONS

blk.—adjustable block.

b. p.—binding post through which the levers are connected to one pole of battery.

fl. sup.—metal support attached to under side of floor and resting on slender pin driven into side of lever bar (*p. br.*).

lr. sup.—metal support for fulcrum of lever.

p. br.—paired bars of lever.

s. br.—single bar of lever which carries the counterweight (*wt.*).

tr.—truss-like frame attached to floor to prevent tipping of latter.

tr. br.—transverse bar of lever

up.—upright posts which support the wire sides and top of the cage independent of floor.

wr.—wire connecting platinum contact (*pl. pt.*, fig. A) through the fulcrum nail (*ful. nl.*, fig. B) and one of the metal supports (*lr. sup.*) with the binding post (*b. p.*).

wt.—counterweight.

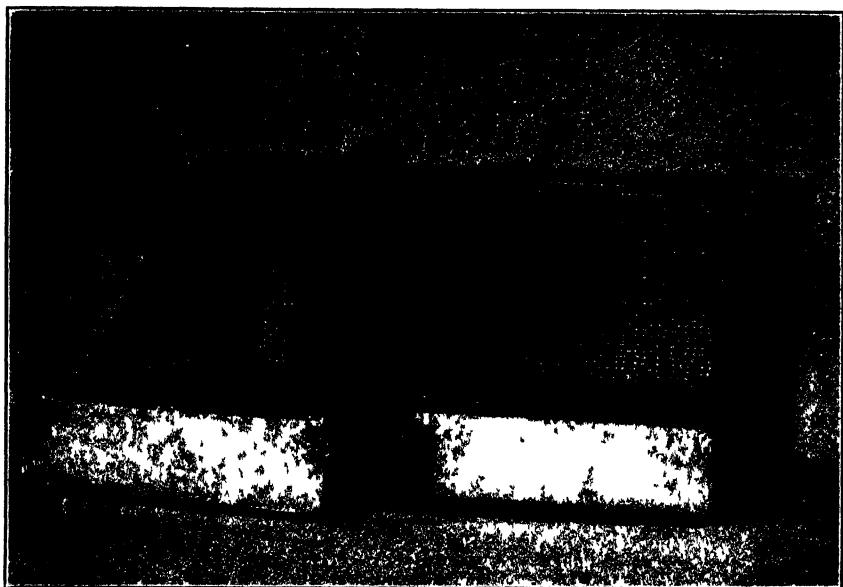


Fig. 1

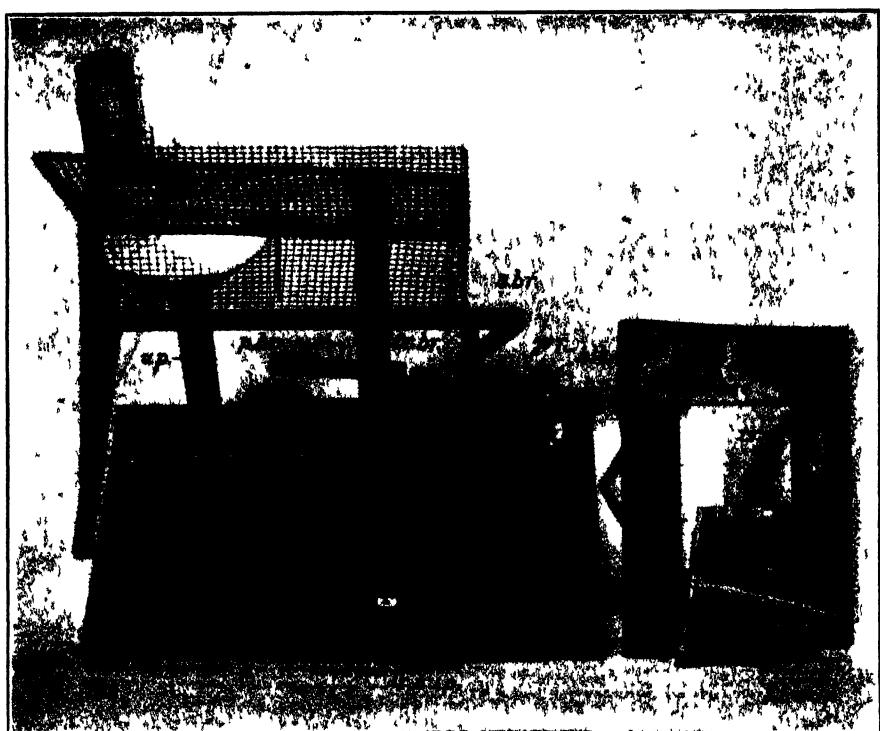


Fig. 2.

PLATE 14

Figs. 3 and 4. Other views of cage and recording apparatus shown in plate 13.

ABBREVIATIONS

blk.—adjustable block.

b. p.—binding post through which the levers are connected with one pole of the battery.

fl. sup.—metal support attached to under side of floor and resting on slender pin driven into side of lever bar (*p. br.*, pl. 13).

lr. sup.—metal support for fulcrum of lever.

tr.—truss-like frame attached to floor to prevent tipping of latter.

up.—upright posts which support the wire sides and top of the cage independent of floor.

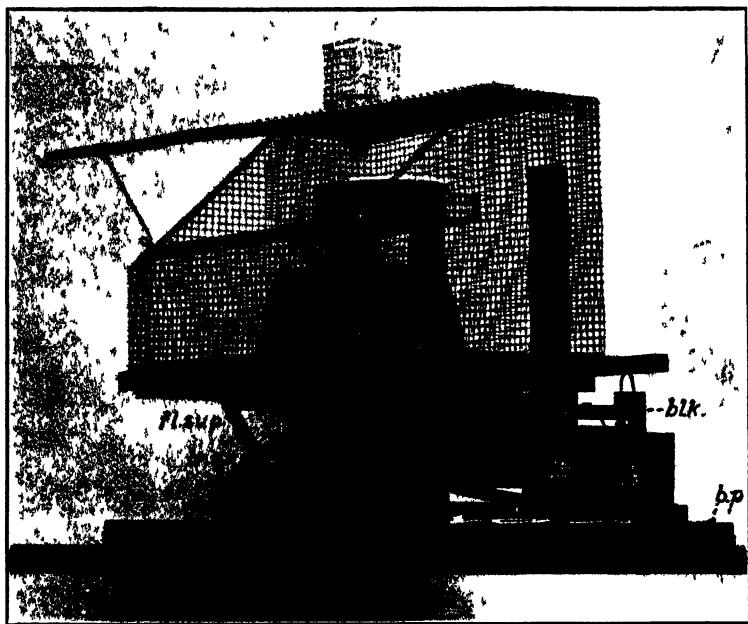


Fig. 3

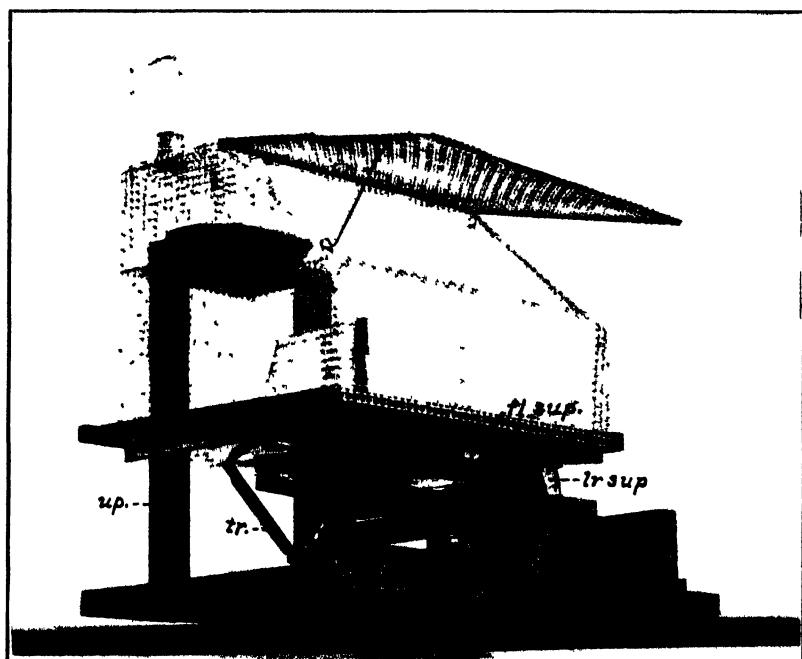


Fig. 4

PLATE 15

One cage of recording apparatus showing connections with the signal magnets, the pointers of which mark the excursions of the floors on the smoked paper of the drum of the chronograph. Three such cages are arranged to make their records on one chronograph.

ABBREVIATIONS

- blk.*—adjustable block.
- b. p.*—binding post through which the levers are connected to one pole of battery.
- c. wr.*—wire connecting the supporting frame of signal magnets to other pole of battery.
- lr. sup.*—metal support for fulcrum of lever.
- lt. br.*—light bar which in connection with the frame (*tr.*) attached to the floor prevents the latter from tipping.
- tr.*—truss-like frame attached to floor.
- wt.*—counterweight.

Contact between the platinum points (*pl. pt.₁*, and *pl. pt.₂*, figs. A and B) completes the circuit, a part of which is formed by one of the coiled wires seen in plate 15. Each lever has its platinum contacts and is connected with one of the signal magnets by one of the coiled wires. (See description, pp. 109-110.)

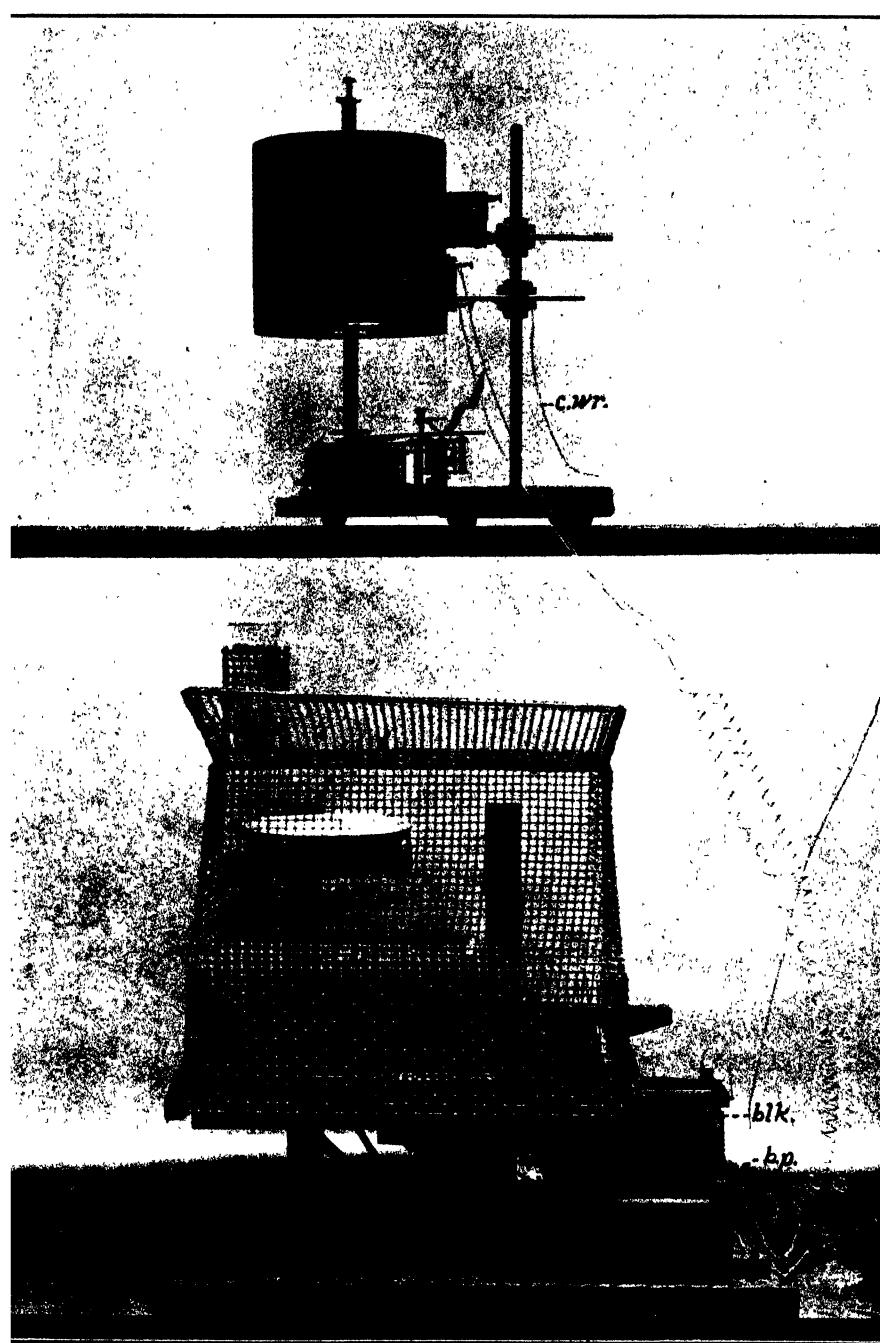


Fig. 5.

PLATE 16

Fig. 6. Front view (side away from the operator) of constant-temperature box for microscope. The glass front, which is invisible in the photograph, is in place and the apparatus inside is seen through the glass. A large 50-degree thermometer (white) is suspended from the glycerine-filled tube of the regulator. The bulb of another rests on the stage of the compound microscope in contact with the circulation slide.

Fig. 7. Rear view of the constant-temperature box. Between the microscopes lies the small (white) rubber tube through which the air of the waste bottle is exhausted and the current started in the slide. The drawing shelf and camera mirror are at the right.

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[MARK & LONG] PLATE 10

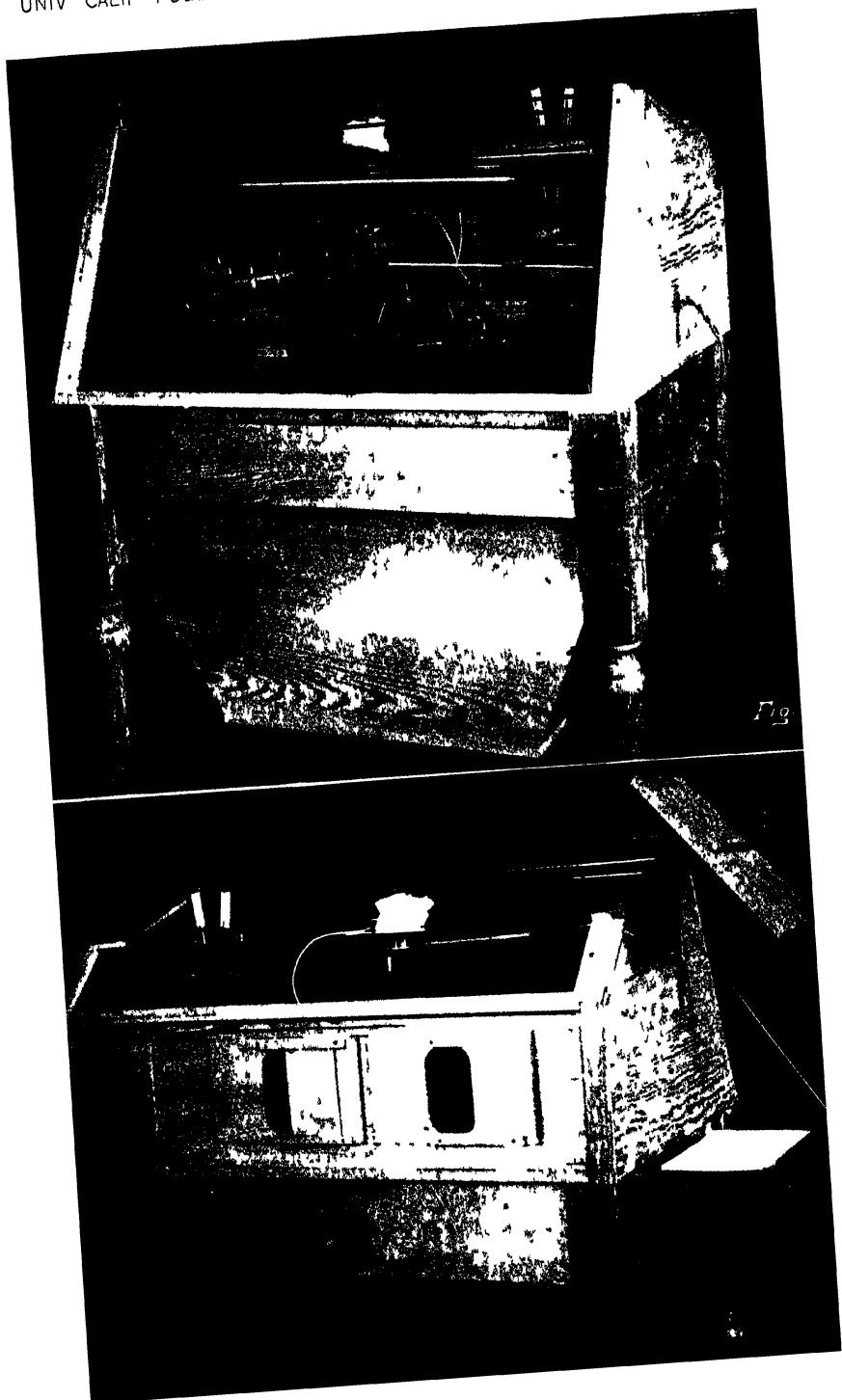
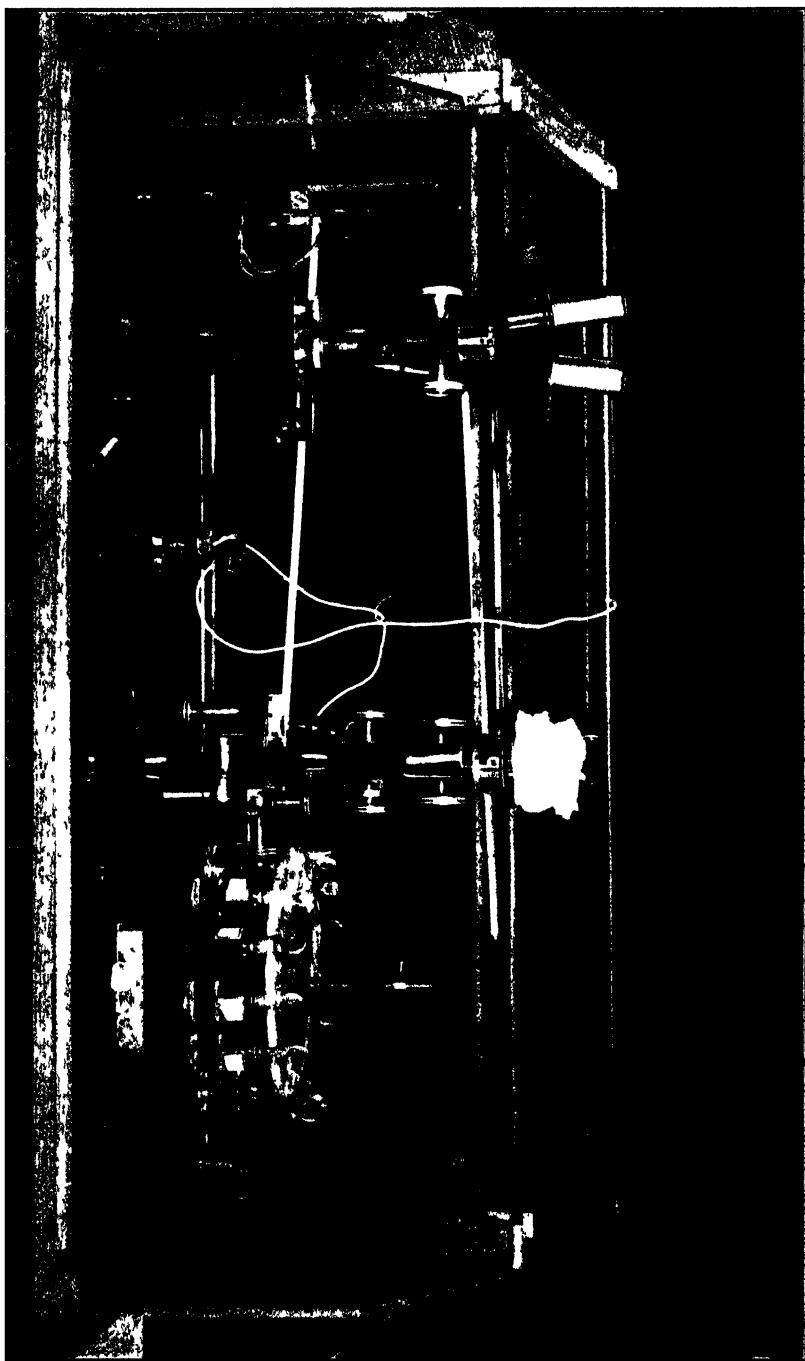


PLATE 17

Fig. 8. Interior of constant-temperature box as seen from behind after removal of the back. At the ends of the box the outer wooden and inner glass walls remain, while a part of the inner wooden is removed with the wooden back and glass top behind the microscopes. The two thermometers as in plate 16. The regulator, shown in figure F (p. 115), is at the left. The slide on the microscope stage is partly obscured by the mechanical stage, but the glass and rubber tubing, as shown in figure K, can be seen passing to one of the bottles at the right and to the waste bottle at the left. The exhaust rubber tube is withdrawn from the hole in the back of the box and is seen hanging over the glass roof and down in front.

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May 28, 1912

OXYGEN AND POLARITY IN TUBULARIA

BY
HARRY BEAL TORREY

It is a familiar fact to students of regeneration that in the regeneration of a segment cut from a stem of *Tubularia*, two hydranths are produced, one at each end of the piece (which is then termed heteromorphic), and that the distal hydranth appears earlier than the proximal. It is also well known that the development of the proximal hydranth can be accelerated by ligating the stem at almost any level.

According to Loeb (1904) this acceleration is connected causally with the diversion by the ligature of the currents circulating in the stem. I have attempted to show (1910), however, that it is due to quite another effect of the ligature, namely, the suppression of the regeneration of hydranths at the ligature on either side owing to an inadequate supply of oxygen at these points. The same proximal acceleration, associated with the same suppression of distal development, may be produced, as Loeb (1906) long ago pointed out, by burying the distal ends of the stem segments in sand. The proximal ends thereupon produce hydranths more rapidly than would have been the case had oxygen had free access to the distal ends. Loeb's surmise that "lack of oxygen is responsible for the fact that no polyp can be formed except at a free end of a stem, since the chitinous surface of the stem is very little permeable for oxygen," is clearly supported (see Torrey, 1910) by the following facts: (1) in *Corymorphia*, the stem is naked, and hydranths do develop *at the ligature*, that is, *immediately below it*; (2) in *Tubularia*, development can be suppressed at either end of the stem by slipping over

that end a glass cap, the suppression of the distal hydranth being coupled with an acceleration in the development of the proximal hydranth. The latter experiment is open to the possible objection that while preventing oxygen from diffusing inward, the glass cap might hinder the diffusion of gases from the stem outward.

A recent experiment, however (performed during a laboratory course in experimental zoology with the coöperation of several students) shows that this objection is not valid, and points conclusively to the supply of oxygen as the essential factor in determining the result.

The method employed consisted in separating by a partition two bodies of sea water that should differ only in the absence of oxygen from one of them, and then passing segments of *Tubularia* stems through perforations in the partition so that approximately equal lengths should project on either side of it, their distal ends being immersed in the deoxygenated water. The simple device used to obtain these conditions was composed of a small battery jar and, fitting snugly into it, a crystallizing dish whose bottom had been removed and a sheet of soft paraffine about 5 mm. thick substituted for it. A portion of water boiled a few minutes to remove the contained oxygen completely filled the battery jar below the paraffine plate. Another portion of the same boiled water, but aerated by pouring from one dish to another, almost filled the crystallizing dish above the paraffined plate. The *Tubularia* stems were so placed that their distal ends projected downward into the de-aerated water, their proximal ends upward into the aerated water. As a control, the previous conditions were duplicated with the difference that aerated water only was used.

Accordingly, two sets of nine pieces each, approximately 2 cm. long and equal in size and vigor, were arranged as described. Sixteen hours later the control pieces possessed six distal, but no proximal hydranths; the other pieces, on the contrary, possessed two proximal but no distal hydranths. Four hours later, seven distal hydranths and six proximal had appeared in the control; on the other pieces there were now five proximal, but still no sign of distal hydranths. Three hours later the control pieces were apparently in the same condition, while in the other dish a

sixth proximal hydranth had emerged and a seventh was emerging. In the same dish, sixteen hours later, all nine proximal hydranths were out, but still no distals; nor did distals show any sign of developing in the de-oxygenated water for two days longer, when the experiment terminated. The control pieces ultimately developed nine distal and seven proximal hydranths, two failing to develop proximally.

It is obvious from these brief records that not only was lack of oxygen hindering the development of the distal hydranths in one set of stems, but the proximal ends of these stems were developing more rapidly in consequence; and this when all possible influence of ligatures or contact stimuli had been removed.

Transmitted April 22, 1912.

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